Skeletal remains of Phoebodus politus Newberry 1889 (Chondrichthyes: Elasmobranchii) from a Famennian Konservatlagerstätte in the eastern Anti-Atlas (Morocco) and its ecology

Frey, Linda ; Coates, Michael ; Ginter, Michal ; Klug, Christian

Abstract: The Devonian chondrichthyan Phoebodus (Newberry 1889) has long been known from isolated teeth recovered from a wide variety of fossil localities, ranging from the Middle Devonian to the Upper Missippian (Ginter et al. 2010). Here we provide a preliminary report of the first discovery of substantial, partly articulated skeletal and dental remains of a phoebodont, Phoebodus politus, from Famennian outrops of the eastern Anti-Atlas of Morocco. Initial comparisons support the hypothesized close relationship of pheobodonts with the Upper Mississippian chondrichthyan Thrinacodus gracia (Grogan Lund 2008, Ginter et al. 2010). Both taxa exhibit an anguiliform body and elongate slender cranium. However, P. politus also exhibits dorsal fins with ctenacanth-like fin spines, echoing informal records of similar fin spine and tooth associations from the Famennian of Alaska (Maisey, in Ginter et al. 2010). This Moroccan material represents an important addition to the limited data set of Devonian chondrichthyans. As such, these data will provide a valuable test of recent phylogenetic hypotheses (Pradel et al. 2011; Coates et al. 2017) and addition to analyses of early gathostome diversity and disparity before and after the end Devonian Hangenberg Event (Friedman Sallan 2012). Among living elasmobranchs, Chlamydoselachus uniquely displays a body shape, snout form and tooth morphology resembling those of P. politus. Acknowledging that the structure and likely biomechanics of the axial skeletons and jaws of these widey separated genera differ considerably, we nevertheless suggest that Chlamydoselachus (Ebert Compagno 2009) provides the best available living model for understanding the ecomorphology of this remarkable, late Devonian comparator.

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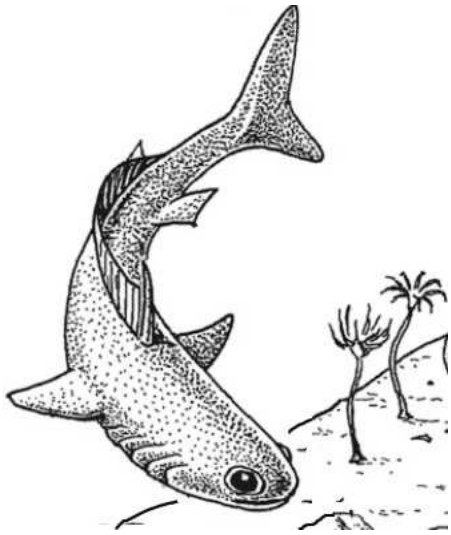
Honoring Susan Turner

Conference Abstracts and Field-trip Guidebook



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Conference logo: Castle at Chęciny and early vertebrates

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14th International Symposium on Early and Lower Vertebrates
Chęciny, Poland, 3-8.07.2017

Organised by

Instytut Geologii Podstawowej, Wydział Geologii, Uniwersytet Warszawski
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and

Stowarzyszenie Delta (Delta Association)

Organising Committee

Michał Ginter and Piotr Szrek

Patrycja Dworczak, Roksana Skrzycka, Piotr Skrzycki, Olga Wilk

General schedule

3.07. : Registration in Warsaw, evening ice-breaking party
4.07. : Travel to Chęciny. Zachełmie Quarry. Opening session.
5.07. : Sessions. Sightseeing at Chęciny.
6.07. : Sessions. Wietrznia Quarry. Conference dinner.
7.07. : Field trips, Ujazd and Płucki. Evening grill.
8.07. : Return to Warsaw.

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PIOTR SZREK

Introduction

Fifty years of symposia on Early/Lower Vertebrates

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In the last 50 years since 1967 thru 2017 (Schultze 2005), 14 symposia on Early/Lower Vertebrates have been held. In the beginning, Erik A:son Stensiö was honored with a Nobel Symposium in Stockholm. In 1972, the Linnean Society, London, honored Erik A:son Stensiö and Erik J:son Jarvik with a symposium. This is followed in 1976 with the I. International Colloquium on Middle Palaeozoic Fishes in Tallinn, Estonia (Soviet Union at the time). At this colloquium, the idea to have regular meetings every four year was proposed. Unfortunately, the suggestion was not followed. The next meeting was arranged seven years later in Australia with the initiative of Ken Campbell. The fifth symposium was 20 years after the first, the 11th 40 years and the 14th 50 years after the first.

Proceedings of the symposia were published in different forms except for the 2nd and 13th symposium. The most important proceedings are those of the second symposium (*The Interrelationships of fishes* [crown gnathostomes]), a volume, which only partially reflects the interest of the group. The two first symposia fall in the beginning time of cladistics within the English-speaking community, but they show little of cladistics, even though G. Nelson and R. Zangerl were present at both symposia. The first symposium finds L. Brundin as a lonely voice for Hennig's system. In the second symposium, some presenters used a cladistic approach with questionable results as discarding the Holostei or splitting the teleosts in two separate lines at the base. All the following proceedings contain descriptions and analyses of Paleozoic vertebrates.

The symposia have strengthened the interaction between paleoichthyologists and have helped international correlation programs. The largest number of participants in each symposium has come from the organizing country with the exception of Brazil 2004 and Sweden 2007. We were hopeful in 1976 to start a biostratigraphic program and planned a cooperation in Podolia, which did not work out at the time of the Cold War. Such cooperation started after the end of the Soviet Union with IGCP 328 (S. Turner and G. Young) followed by IGCP 406 (M. Wilson and T. Märss) and IGCP 491 (M. Zhu and G. Young). The driving force in the programs was S. Turner. She started a communication publication (Ichthyolith Issues), where three special volumes present the abstracts of symposium 11 (Ichthyolith Issues Spec. Publ. 10), 12 (Ichthyolith Issues Spec. Publ. 12) and 14 (Ichthyolith Issues Spec. Publ. 13). The special mentioning of Sue Turner in this symposium, follows the honor to E. Stensiö (symposia 1 and 2), E. Jarvik (symposium 2), V. Karatajute-Talimaa and E. Mark-Kurik (symposium 11), and D. Goujet (symposium 13).

Schultze, H.-P. 2005. The first ten symposia on early/lower vertebrates. – *Revista Brasileira de Paleontologia,* **8** (20): V-XVIII.

Fifty years of international symposia on early/lower vertebrates : honoring Dr. Susan Turner, colleague, friend and mentor

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For us, and for the early vertebrate community of scientists who meet ca. every four years in an international symposium devoted to mostly Palaeozoic fish, Dr. Susan Turner is known as Sue. She was trained in geology at Reading University, England in the 1960s, specialising in vertebrate palaeontology. In 1967 she became research curator in the departmental museum, and began her doctoral research — this was the same year that the first symposium on early vertebrates was held at Stockholm, Sweden as a Nobel Symposium, devoted to 'Current problems of lower vertebrate phylogeny' (Schultze, 2005). She first participated in an early vertebrate symposium in 1976 in Tallinn, Estonia (then in the USSR), where she presented an oral communication on Silurian-Devonian thelodonts (Turner, 1976), and when one of us (AB) met her for the first time.

She concentrated her doctoral work on jawless fish, and in particular thelodonts, in the frame of biostratigraphy in the classic Silurian-Devonian sequence of the Welsh Borders. In 1971, she became Museum Assistant (Curator in Geology) in the Hancock Museum, Newcastle-upon-Tyne. She was a Temporary Scientific Officer at the Nature Conservancy Council, U.K.; and also obtained the Museums Association of the U.K. Diploma in 1979. Her Ph. D. thesis (begun under the supervision of Bev. Halstead at Reading) was obtained in 1984 at University of Newcastle-upon-Tyne under the supervision of Prof. T.S. Westoll (Turner, 1984). However, due to the economic and political situation of the U.K. in the 1970s, Sue could not get a more permanent position. Australia - and her future husband, Tony Thulborn - beckoned, and so she emigrated to Australia and joined the Queensland Museum in Brisbane in 1980 as an Honorary Research Fellow. She then occupied various temporary positions including Secretary, Council of Australian Museum Directors, Queensland Museum; Research Fellow on grants, Queensland Museum; ARC Australian Research Fellow; DAAD Visiting Professor, Institut für Geologie und Paläontologie, Universität Hannover, Germany; "chercheur associé", CNRS, Université de Lille, France; Honorary Research Associate, New Brunswick Museum, Canada; Visiting Professor, University of Lanzhou (Paleobotany Section), China; Visiting Researcher, University of Tübingen, Germany, and Natural History Museum, London, U.K.; Adjunct Research Associate, Monash University; Honorary Research Associate, Curtin University… She is presently Honorary Research Fellow, Queensland Museum, and Honorary Adjunct, Monash University, and also self-employed scientific consultant and English editor for the Chinese Academy of Geological Sciences (*Acta Geologica Sinica*) and University of Lisbon, Portugal (*Journal of History of Science and Technology*). Sue was also (and is still) much involved in UNESCO-IGCP, Global Geoparks and INHIGEO programs. In particular she co-led with great success IGCP Project 328 "Palaeozoic Microvertebrates" (1991-1996) (Blieck & Turner, 2000), and instituted *Ichthyolith Issues*, the early vertebrate community newsletter (1988-2003).

Her scientific work concentrates on agnathan and chondrichthyan fish, with special interest in thelodonts, basal sharks (e.g. *Doliodus*, *Protodus*, *Mcmurdodus*), and other groups (e.g. gyracanths, xenacanths). She has focused her 50 years of research on systematics, biostratigraphy (especially the use of agnathans in dating and correlating mid-Palaeozoic strata), and palaeobiogeography (with a first *Nature* paper on the closure of Iapetus in 1970). Migrating to Australia, she discovered new taxa, notably mid-Palaeozoic thelodonts and sharks, based on microfossils. A master work was the *Handbook of Paleoichthyology*, volume 1B, published with T. Märss and V. Karatajūtė-Talimaa (Märss *et al.*, 2007). One recent important work challenged the hypothesis that conodont animals were vertebrates (they are not!) (Turner *et al.*, 2010). Her field experience includes work on four continents, with description of fossils from many countries besides the U.K. and Australia (Antarctica, Bolivia, Canada, China, Baltic States, France, Indonesia, Iran, Norway, Russia, Saudi Arabia, U.S.A. …). Sue is deeply interested in the history of women as geologists and the history of geological sciences in general, and has published extensively on these topics (e.g. Turner & Cadée, 2006). Last, but not least, Sue has mentored dozens of postgraduates over the years, both officially and unofficially, including quite a few of the participants at this conference. Outside science, Sue is a confirmed artist, enjoying in particular oil pastel painting. We thank her for her willingness to share her knowledge with us all.

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Early/Lower Vertebrates Meetings: Sue Turner and her impact on palaeoichthyology in the Middle East

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My first encounter with early vertebrates backs to 1998, when as a postgraduate student to the University of Isfahan, I met John Long whom I can call, my first teacher on early vertebrates. He directed me to micro-world of early vertebrates where I could find my interest in chondricthyans. Soon after, it was appeared that numerous thelodont and acanthodian scales were found in my collections and had to deal with them! In that time lack of enough publications made me difficult to work on. However, I needed to get some more information and then just found blue/green *Ichthyolith Isuues* as hard copies, which were sent earlier by Sue Turner to the Geology Department. By reading these it was much easier to go through a list of earlier and key publications, and so. She published her first article much earlier on Iranian thelodonts from Alborz Mountains, and Saudi Arabia (Turner and Janvier, 1979, Boucot et al 1989), and she knew well how exploring in the Middle East will provide new discoveries and important additions to the world knowledge of early vertebrates and regional geology. I appreciate her dedication, constant supports and tireless efforts which made a positive impact in my scientific career.

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Some brief remarks on Susan Turner and my experiences with the Early/Lower Vertebrates Meetings

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My introduction to Sue Turner and to the Early-Lower Vertebrates series of meetings happened around the same time, in 1999-2000, early in my “career” as an avocational paleoichthyologist.

The library of the University of Colorado at Boulder, where I live, is not bad, but is sadly deficient in its collection of *Ichthyolith Issues*. I was able to obtain hardcopies by writing to

Sue. We met for the first time at the 9th E-L V Meeting in Flagstaff, Arizona, in 2000. The Flagstaff meeting was my introduction to the small and tightly-knit community of Paleozoic paleoichthyologists, of which I now consider myself a part. Since then, our paths have crossed many times, though never in either Brisbane (she always seems to be somewhere else) or in Boulder (no one goes to Boulder). Once, we happened to be visiting the Natural History Museum in London at the same time. I found an odd fossil from the Devonian Hunsrück Slate of Germany. It was labeled as "*Edestus"* but was clearly not even a vertebrate. It had been purchased in the 1930s, and never published on, whether from lack of interest or from embarrassment at being fooled. We managed to have photographs published in both the *Geological Curator* and in the "Mystery Fossil" section of the newsletter of the Palaeontological Association. This got the attention of Derek Briggs (Yale), who managed to appeal to the NHM to have an x-radiograph taken, something that I had not been able to do on my own. He thought that it could be the body fossil of a machaeridian (an armored worm-like invertebrate). However, the x-radiograph showed it to be a trace fossil instead, and nothing further has been published.

International Symposium on Early and Lower Vertebrates in the Holy Cross Mountains, Poland

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In my scientific career I had two dreams: to find *Harpago ferox* teeth in my Polish samples and to organise a Symposium on Early and Lower Vertebrates in Poland. Both dreams are now fulfilled.

When I came back from one year of obligatory duty in the communist army in 1987 and started to work at the Faculty of Geology, I had no prospect for a good Ph.D. subject. I could do echinoids in Tertiary sands and Carboniferous foraminifers in thin sections, but they were too far from my beloved conodonts. And then, a miracle happened. My supervisor, Professor Michał Szulczewski came to me and asked if I wanted to look at fish particles from his Devonian conodont samples. I had absolutely no experience in vertebrates, but I started digging in literature and soon came across the excellent, now already classic paper by Sue Turner in JVP, about Australian mid-Palaeozoic sharks (Turner 1982). That paper opened my eyes and I understood that most of the ichthyoliths in the samples are indeed shark teeth and scales.

I contacted Sue. In those pre-internet times it was not very easy, every exchange of thoughts between us took about a month, but Sue's letters were so full of information that, when I already learned to de-cipher her writing, they were a material for a long study. We first met in Tallinn, during that excellent conference in 1989, when the Baltic republics were preparing for independence, and we spent a long time talking about fossil sharks. Soon Sue became my unofficial supervisor, she opened to me the world of Palaeozoic fishes, taught me how to write scientific papers in English, patiently correcting my early drafts. She went so far as to invite me to Brisbane, covering all my expenses, including jet-about holidays in Singapore. That travel to Australia formed a solid ground on which I built my future work.

But back to *Harpago*. When I saw its illustrations in Sue's paper, it totally conquered my imagination. And how happy I was when very soon, in one of the samples from the Famennian of Łagów in the Holy Cross Mountains, I found a shiny, anthracite-black, almost complete tooth of what is now called *Thrinacodus tranquillus*, but at that time was an undoubted *Harpago ferox* Turner, 1982. I confess, I have never accepted that Sue had to abandon the name *Harpago* for *Thrinacodus*...

In the early nineties, organising an international conference seemed to me something unimaginable and I perceived the people like Otto Walliser who organised our Gross Symposium (1993) or Philippe Janvier and Alain Blieck who led the organisation of the huge Early-Lower Vertebrates Symposium in Paris (1995) as heroes. However, Sasha Ivanov who invited us to St. Petersburg in 1997 has shown to me that an ordinary mortal can make a perfect conference with little resources. So, the next year, I dared to organise a meeting under the auspices of IGCP 406 (a successor project of the very successful IGCP 328 Palaeozoic Microvertebrates, invented and co-led by Sue Turner) in Warsaw (1998). I liked it so much that organising such events went into my blood. With Vachik Hairapetian we prepared a tiny meeting of IGCP 491 in Armenia (2005) and with Piotr Szrek the "Evolution and diversity of chondrichthyans" meeting in Warsaw (2008).

However, all these conferences did not belong to the highly esteemed series of International Symposiums on Early and Lower Vertebrates. So this was something that I wanted to do before I retire. I did not participate in many such meetings, only three: Paris (1995), Flagstaff (2000) and Uppsala (2007), but all of them were very important for the early-lower vertebrate society and for me. I particularly remember a moment in Flagstaff, when Hans-Peter Schultze, inspired by John Maisey, kindly invited me to write a volume of the Handbook of Paleoichthyology dedicated to Palaeozoic shark teeth. This invitation has definitely changed my scientific life.

The concept of the ISELV in Poland started to crystallise when the Faculty of Geology, University of Warsaw, began the construction of the European Centre of Geological Education in a former dolomite quarry at Rzepka Hill near Chęciny, in the heart of the Holy Cross Mountains. At once we understood that, if the construction was successfully finished, it would be a perfect place for such an event and the Faculty would benefit of that. The ECEG was officially opened in autumn 2016. The Polish team planned the Symposium for 2018 (as a continuation of 1998 and 2008 conferences) and Piotr Szrek presented our proposition in Melbourne (2015). However, it turned out that our Chinese colleagues had the same idea, so the participants (not without some opposition) split the Symposium in two: Poland in 2017 and China in 2019. Piotr called me from Australia asking what I thought and I, rather reluctantly, agreed. But soon we have realised that it was a very good decision: our conference is exactly 50 years after the first one, Stockholm (1967). Much later, Alain Blieck proposed, and we gladly agreed, to dedicate this meeting to Sue Turner and her work.

And so it is: the 14th International Symposium on Early and Lower Vertebrates, Chęciny, Holy Cross Mountains, Poland, 2017, honouring Dr Susan Turner, in the 50th anniversary of the first symposium.

You are most welcome!

Sue at the "Evolution and diversity of chondrichthyans" meeting in Warsaw, July 2008.
Photo M. Bieńkowska-Wasiluk.

Major works by Sue Turner

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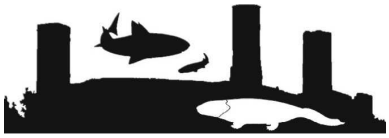

Tesseraspidiformes (Vertebrata: †Pteraspidomorphi: Heterostraci), a group of enigmatic early vertebrates

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The Pteraspidomorphi is a group of jawless vertebrates that lived from the Early Ordovician to the Late Devonian (ca. -470 to -372 My). The head is generally covered by a bony dermal armour organized into large dorsal and ventral plates, and the trunk and tail by scales. They had no paired or midline fins other than the caudal fin. They are united by the presence of acellular bone (aspidin) in the armour. Four clades are included in the Pteraspidomorphi: the Arandaspida, Astraspida, Eriptychiida, and Heterostraci (*sensu* Janvier, 1996). Heterostraci are concerned here. They are known from the Lower Silurian to the Frasnian (Upper Devonian), mainly in sedimentary series originated from Laurentia, Avalonia and Baltica palaeocontinents in the Silurian, and the Old Red Sandstone Continent and Siberia in the Devonian. They have a single paired external branchial opening, and a cancellous (honeycomb-stitch-like) dermal bone. They were diverse, with more than 300 species described to date (but their diversity or specific richness is under evaluation). The best known and most common heterostracans are the Cythaspidiformes (including amphiaspids) and the Pteraspidiformes (including psammosteids). In addition to these two major clades there are a number of minor groups whose affinities are uncertain, viz., traquairaspids, cardipeltids, corvaspids, ctenaspids, *Nahanniaspis*, and various tesselated taxa (tesseraspids, *Lepidaspis*…). One of the questions to answer is as follows: is a tesselated pattern of the armour plesiomorphic for heterostracans ?

Here we focus on new material of tesseraspids (Tesseraspidiformes) from the Severnaya Zemlya archipelago, in Russian Arctic. It comes from the uppermost Severnaya Zemlya Formation (Lochkovian, Lower Devonian), where it has been collected in association with corvaspids, articulated and disarticulated acanthodians, and rare but big specimens of osteostracans. The tesseraspid material is not abundant, and most often preserved as a "patchwork" of broken fragments of head carapaces, except a few partly articulated specimens. Among the latter, we redescribe in detail the holotype of *Tesseraspis mosaica* Karatajūtė-Talimaa, 1983, whose head carapace is preserved as a flattened muff of adjacent platelets. All the other partly articulated specimens are of bigger size than the holotype, so that we are not sure whether or not they belong to the same species. So, we keep an open nomenclature for these specimens, that is, *Tesseraspis* sp.

This material is compared to the already published tesseraspid taxa, viz., *T. tessellata* Wills, 1935 (type species); *T. mutabilis* (Brotzen, 1934); *T. toombsi* Tarlo, 1964; *T. orvigi* [*sic*] Tarlo, 1964; *T. denisoni* Tarlo, 1964; and *T. talimaae* Tarlo, 1965. All the published tesseraspid taxa are known after rare material. This material is always incomplete: no trunk and tail in connection with head carapaces are known. So, the intraspecific variability is unknown, and the distinction between species is mainly based on the detail of the

"ornamentation" (or better superficial ultrastructure) of the platelets of the head carapaces, which is unsatisfactory. Comparisons are also made with other tesselated taxa such as *Lepidaspis*, *Aserotaspis*, *Oniscolepis / Strosipherus*, *Kallostrakon*, *Aporemaspis*, « *Weigeltaspis* » … This research is made in the frame of the Handbook of Paleoichthyology (H.-P. Schultze ed., G. Fischer Verlag, vol. 1A, in collaboration with D.K. Elliott and Ph. Janvier).

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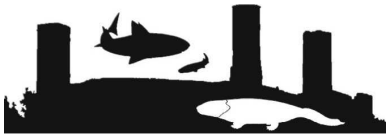

Anatomical Networks Analysis of the skull roof of placoderms

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Connections among the component parts of complex anatomical structures are one of the key source of information in macroevolutionary studies identifying homologies or assessing phenotypic and morphological changes in vertebrates (Riedl, 1978; Woodger, 1945). The pattern of connections (e.g., the particular arrangement of bones connected by their sutures) is established during development; variations of this pattern of connections among anatomical parts promote morphological changes under developmental or topological constraints (see Depew *et al.*, 2008).

Network Theory is the mathematical field that studies complex systems of interacting parts, based on their pair-wise relations between elements. It is widely used in many disciplines from ecology to genomics, including paleontology (Rasskin-Gutman & Buscalioni, 2001). For example, the analysis of anatomical networks (AnNA) has proved

ideal to study the connectivity patterns of the skull of tetrapods (Esteve-Altava *et al*., 2013, 2014, 2015). However, it has never been applied to study early vertebrates, although other sort of analyses of their skull roof patterns were carried out (Thomson, 1995).

Here, we use the AnNA to quantitatively characterize the connectivity pattern of the skull roof of placoderms, the earliest jawed vertebrates. Our results show that the presence of three connectivity modules is the most widespread condition, whereas in specific groups such as Ptyctodontida and Antiarchi there are only two lateral modules. Interestingly, a fourth module appears in *Entelognathus primordialis* and *Qilinyu rostrata*, whose mandibles present osteichthyan-like bones (Zhu *et al.,* 2013; Zhu *et al.,* 2016). This entices us to consider that the appearance of these bones could be related to a reconfiguration of the skull architecture. We also evaluated the presence of phylogenetic trends in the variation of network parameters, commonly used as proxies of morphological complexity. We found an increase in the anatomical complexity of the skull as the number of bones decreases in the group (i.e. between the most basal and most crownward placoderms), as previously reported by Esteve-Altava *et al.* (2013)' study of the Williston's Law in tetrapods.

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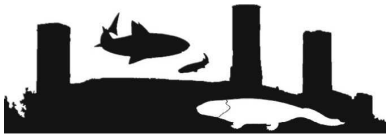

The first vertebrate microremains from the upper Silurian of the Holy Cross Mountains, Poland

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The Silurian strata of the Łysogóry region in the northern Holy Cross Mountains have been reviewed and revised during the last decade (e.g. Kozłowski, 2008; Kozłowski & Munnecke, 2010), but reports of vertebrates have remained scarce from Polish sections (e.g. Märss, 1997). This region presents a different depositional setting compared to the northeastern parts of the Baltic Basin, and the majority of the sequence is composed of non-vertebrate producing, deep-water sediments (Kozłowski, 2008). However, parts of the succession preserve shallow-marine deposits with intercalations of carbonates containing vertebrate remains (Kozłowski & Munnecke, 2010). Here, we present vertebrate microremains of two samples taken from an open-marine limestone and a marginal-marine oolite in the Winnica and Rzepin localities respectively. The sections are largely coeval and display similar faunas composed of "nostolepid", "gomphonchid" and poracanthodid acanthodians, thelodonts *Thelodus parvidens* and *Th. trilobatus*, as well as fragmentary anaspid remains reminiscent of *Liivilepis*. However, only the oolitic sample contains osteostracan fragments and the thelodont *Paralogania ludlowiensis*, which provides a striking example of the specific environmental preferences postulated for this taxon by Kaljo et al. (2015). This study is the first extensive description of vertebrate faunas from outcrops in the Holy Cross Mountains, and functions as a preliminary study of vertebrate distribution in this area.

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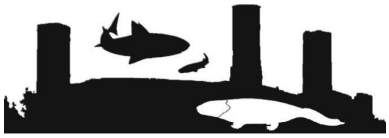

The Early Devonian ischnacanthiform acanthodian *Ischnacanthus gracilis* from the Midland Valley of Scotland

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Ischnacanthus gracilis (Egerton, 1861), the only ischnacanthiform acanthodian from the Lower Old Red Sandstone of Scotland, is known from hundreds of specimens in institutional collections worldwide. Despite this relative abundance, morphology and histology of its skeletal elements have rarely been investigated. Surface details of spines, dental elements, and scales are often not visible in specimens because they are usually split through the middle. We have examined a broad size range of fish, from 35 mm to 250 mm long. Several intact (not split) specimens have been collected in recent years and acid-prepared to show fine details of the dermal and dental elements. We have also used scanning electron microscopy of scales, jaws and dental elements, denticles and fin spines, and serial thin sectioning of articulated specimens, to document their structure. Some of our notable observations include: identification of ventral lateral lines, double-layered calcified cartilage forming the jaws, and the probable occurrence of extraoral bi- and tri-cuspid denticles on the jaws of most fish. We are also analysing the size range, body proportions and dentition of institutional specimens to determine if there could be more than one species represented in the Midland Valley localities.

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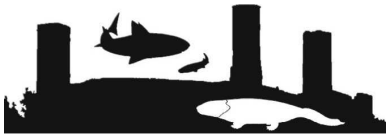

Acanthodians from the Lower Devonian (Emsian) 'Placoderm Sandstone', Holy Cross Mountains, Poland

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The Lower Devonian 'Placoderm Sandstone' in the Holy Cross Mountains (HCM) is filled with abundant impressions of disarticulated vertebrate remains. The only acanthodian macroremains named to date are fin spines of *Machaeracanthus polonicus* Gürich, 1901. Fin spine impressions in slabs from the Winna Formation at Podłazie Hill (near Daleszyce) in the southern HCM, and also the Barcza Formation (upper Pragian-lower Emsian) at Barcza Quarry and Zagórze Formation (middle-upper Emsian) at Bukowa Mountain in the northern HCM, reposited in the University of Warsaw, Polish Geological Institute-National Research Institute, Warsaw, and Natural History Museum, London collections, have been cast and studied in order to better document this poorly known taxon. As noted by Burrow *et al*. (2010) in other *Machaeracanthus* species, we have found that *M. polonicus* has two different morphotypes of spines. Our investigations show that the fin spine assemblage includes *Onchus overathensis* (Gross, 1933) as well as *M. polonicus*. The affinities of *O. overathensis* are reassessed, and it is here considered to be a diplacanthiform, and reassigned to the genus *Striacanthus*. Acanthodian scapulocoracoids have also been identified, as well as tightly spiralled toothwhorls which could be from an acanthodian.

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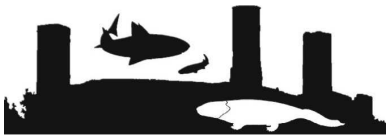

The Cleveland Shale fauna and the Devonian–Mississippian transition in Ohio and Pennsylvania (U.S.A.)

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The Famennian fish fauna from the Cleveland Shale Member (Ohio Shale Formation) represents a 160-year collection effort starting in the mid-19th Century and continuing today. Three periods of increased research include 1857–1909 with such notable names as Newberry, Claypole, Dean, and Hussakof. This was followed in the 1930-1947 period with the work of Dunkle and Bungart. Since 1964 there has been a steadily increasing interest in the Cleveland Shale fauna. Hlavin (1976) completed the first comprehensive review of the fauna and noted 40 vertebrate taxa. This number has grown to 66 taxa (Carr & Jackson, 2008), more than double the next-most speciose Famennian fauna (32 species, Tafilalt, Morocco; Lelièvre, 2003), and our knowledge of the Cleveland Shale fauna continues to grow. This growth includes a new genus and species of selenosteid arthrodire, other new species in the shoreward laterally-equivalent Chagrin Shale Member (Ohio Shale Formation),

and the preparation of new material for taxa that are only know from limited or incomplete specimens. The discovery of placoderm egg cases in the Cleveland Shale (Carr, 2010a) demonstrates the equal antiquity of oviparity and viviparity among the basal gnathostomes. The pelagic nature of the large arthrodires (Carr, 2010b) associated with these egg cases suggests the possibility of arthrodiran hatcheries in the eastward shallower parts of the Appalachian Basin. An interesting note regarding the diversity of the Cleveland Shale fauna is the lack of any analysis of microvertebrates, although bone beds and lag deposits have been identified in the field.

The Cleveland Shale was considered at one time to represent the latest Devonian with the overlying Bedford Shale and Berea Sandstone Formations representing the earliest Mississippian (e.g., Lewis, 1988). This entire sequence, found in the Cleveland, Ohio area and NW Pennsylvania, is now considered to represent the latest Devonian (Brezinski et al., 2010; Baird et al., 2011; Baird, 2013) and is equivalent to the Hangenberg shales and sandstones of the European Hangenberg Biocrisis (Kaiser et al., 2016). Associated with the biocrisis is an episode of end-Devonian glaciation. This is documented in the eastern Appalachian Basin by a succession of glacigenic tillites (Brezinski et al., 2010). In Kentucky, a 3-ton granitic dropstone is embedded within the Cleveland Shale (Lierman et al., 2009) suggesting ice rafting from eastern glaciated regions.

The correlation between the Ohio and NW Pennsylvania sequences with those in the glaciated regions of the eastern Appalachian Basin remains unclear. However, the presence of a series of unit-boundary bone beds and bone-containing lag deposits within the Cleveland Shale offer the opportunity to correlate these units, to tie the Appalachian events to those of Europe, and to document the pattern of extinction for the vertebrates in Cleveland Shale fauna. Sallan & Coates (2010) report both a loss of diversity and a complete restructuring of the vertebrate worldwide communities associated with the Hangenberg Biocrisis; however, they note a lack of clarity in the peri-Hangenberg fossil record. The microvertebrates in the Ohio and NW Pennsylvania sequences may provide the needed clarity. For example, Grogan & Lund (2012: 8) note “no evidence currently exists for cochliodont tooth plates in Devonian deposits…” however; an early analysis of the Corry Sandstone bone bed (a lateral equivalent of the Hangenberg shales in Pennsylvania) demonstrates the presence of cochliodontiform tooth plates. From the base of the Famennian sequence in Ohio (Huron Shale Member, Ohio Shale Formation) to the base of the Carboniferous (Sunbury Shale) there are over 10 stratigraphically distinct bone beds and within the Cleveland Shale a number of bone-containing lag deposits. This regionally confined sequence offers a test of the biological effects of the Hangenberg Biocrisis in the Appalachian Basin as predicted by Sallan & Coates (2010).

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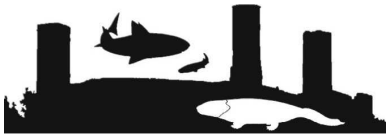

Redescription of *Kolymaspis sibirica* Bystrow 1956 and the affinities of acanthothoracid placoderms

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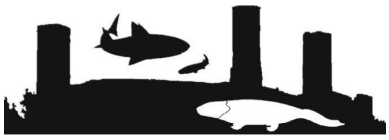
Acanthotoracid placoderms have long been considered primitive among stem-gnathostomes, displaying a combination of both plesiomorphic and apomorphic characters which can help reconstruct the evolutionary history of jawed vertebrates. However, most recent phylogenetic analyses have resolved the group as non-monophyletic, with the two best-known taxa, *Brindabellaspis* and *Romundina,* placed far apart. Indeed, *Brindabellaspis* has been resolved as the sister group of other jawed vertebrates while *Romundina* has been placed closer to the more crownward placoderms such as arthrodires. However, very few acanthothoracids are known from well-preserved endocranial material, making it difficult to investigate their affinity. Here, we redescribe the morphology of the acanthothoracid *Kolymaspis sibirica*,

from the Kolyma Basin, Siberia. Using modern CT techniques and three-dimensional computed reconstruction, we provide the first description of its sensory line system and internal morphology, with emphasis on the orbital and anterior brain cavity morphology. The morphology of the sensory line and brain cavity resembles *Romundina,* particularly in the course of nerves and blood vessel and in the morphology of the labyrinth. On the other hand, *Kolymaspis* shows an elongated snout and nasal capsules placed cavity within the orbit, similar to *Brindabellaspis*. The anatomy of *Kolymaspis* is thus intermediate between these long- and short-nosed "acanthothoracids". A preliminary phylogenetic analysis resolves *Kolymaspis* as the sister group to the antiarchs. Acanthothoracids are resolved as paraphyletic, and arrayed between rhenanids and antiarchs. Placodermi is resolved as monophyletic, with petalichthyids and ptyctodonts resolved as monophyletic. The data thus corroborate recent analyses that resurrect placoderm monophyly, implying dorsally oriented nostrils as a specialization.



3D microstructures of the earliest osteichthyan teeth and life history of the stem osteichthyans *Andreolepis* and *Lophosteus*

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Osteichthyans have evolved a distinctive manner of replacing their teeth by basal hard-tissue resorption. The earliest examples are given by the Silurian stem osteichthyans that are known exclusively from isolated materials, *Andreolepis hedei* from the Ludfordian of Gotland, Sweden (Chen et al. 2016) and Lophosteus superbus from the Pridoli of Saaremaa, Estonia (Chen et al. 2017). We have investigated the organization of these dentitions in 3D with sub-micron resolution using propagation phase contrast synchrotron microtomography. Cyclic shedding teeth occur in both their marginal jaw bones and in tooth cushions that presumably formed an inner dental arcade, but the growth modes differ between the outer and inner dental arcades, and between the taxa. Teeth on the marginal jaw bones are seemingly pre-patterned by the tooth-like first-generation dermal odontodes that are organized in alternate files, but have been partially buried by the overgrowth of younger generations of odontodes. In *Lophosteus*, the oldest shedding teeth are initiated above each of the most lingual first-generation odontodes, while in *Andreolepis* they are added on a more lingual field. The first-generation teeth on the *Lophosteus* tooth cushion have the tip shed but the dentine base retained, whereas those on the *Andreolepis* tooth cushion are shed entirely as are all the replacement teeth. The first-generation biting odontodes consist of orthodentine, while the overgrowing ornamental odontodes of *Lophosteus* have been filled by osteodentine. Secondary dentine has been deposited in *Andreolepis* teeth narrowing the pulp cavity, but the

pulp cavities of all *Lophosteus* teeth are wide and straight. In specimens with the same number of growth arrest surfaces, which indicates the same age, the number of resorption surfaces is at least twice as great in *Lophosteus* as in *Andreolepis*. *Lophosteus* thus has a much faster tooth replacement rate and its teeth have commonly been replaced a dozen of times. The spatial relationship between the growth arrest surfaces and the resorption surfaces not only provides information on the life history, but also allows us to infer the temporal relationship between the development of teeth and jaw bones. The well-preserved hard tissues are comparable with those of crow-group taxa, demonstrating the tissue composition of teeth are conserved in vertebrates; on the other hand, the subtle differences between teeth and odontodes can give clues about the origin of teeth and tooth replacement.

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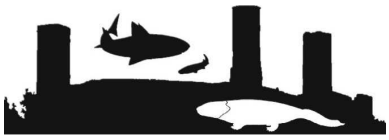
Chen, D., Blom, H., Sanchez, S., Tafforeau, P., Märss, T., and Ahlberg, P.E. 2017. Development of cyclic shedding teeth from semi-shedding teeth: the inner dental arcade of the stem osteichthyan Lophosteus. – *R. Soc. Open Sci.* **4**: 1-21.



New material of an unusual tetrapodomorph fish from the Middle Devonian of central Australia.

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Outcrops of the Middle Devonian Harajica Sandstone Member of the Parke Siltstone in central Australia (Northern Territory) have produced a well preserved fossil fish assemblage, comprising the antiarch *Bothriolepis* sp., the phyllolepid *Placolepis harajica* (Young, 2005), a *Striacanthus*-like acanthodian and the dipnoan *Harajicadipterus youngi* (Clement, 2009). The fifth, and perhaps most intriguing member of this fauna is an as yet undescribed basal tetrapodomorph originally based on several partial skulls and incomplete postcrania in the Australian National University collections recovered in the 1980s and 1990s. Preliminary work by Tim Holland, formerly at Museum Victoria, revealed an unusual combination of features in this taxon, including a long parietal shield relative to the posteriorly broad postparietal, tiny orbits and enlarged spiracular openings (Long, Holland & Young, 2012).

In 2016, a joint expedition from Flinders University and ANU revisited the site and a large quantity of new fossil material was collected and prepared at Flinders University. Of particular importance was the discovery of the first and only complete specimen of the Harajica tetrapodomorph in dorsal view. The find firmly establishes that the previously scattered partial remains constitute a single new tetrapodomorph taxon and provides previously unknown details of the body and fins. A rigorous reconstruction of the entire fish is presented for the first time. A phylogenetic analysis resolved the new form as the most basal member of the Canowindridae, extending the geological range of this endemic Gondwanan clade into central Australia.

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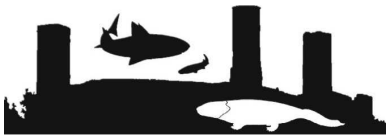

An exceptional 3D coelacanth (Osteichthyes: Sarcopterygii) from the Devonian of Australia and interpretation of fossil cranial endocasts

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Coelacanths are a clade of the 'lobe-finned' fishes (Sarcopterygii), alongside lungfishes and tetrapods. They are iconic sarcopterygian fishes which peaked in diversity during the Carboniferous Period around 330 million years ago, but steadily declined with only two species alive today (*Latimeria chalumnae* and *L. menadoensis*). Most early coelacanth fossils are preserved as compressed specimens and details of their internal cranial anatomy were derived from serial wax sections of one taxon, *Diplocercides*, from the Late Devonian of Germany (Stensiö 1963).

Here we present two specimens of the first exceptionally preserved 3D coelacanth from the Late Devonian (Frasnian) Gogo Lagerstätte of northern Western Australia, which reveals for the first time the cranial anatomy of an early coelacanth elucidated using modern micro-CT tomography (μCT).With advances in tomographic scanning techniques and software for 3D analysis and visualisation, more internal cranial anatomy and endocast data from fossil taxa are informing debates surrounding evolutionary problems of early jawed vertebrates (e.g. Lu et al. 2012; Clement & Ahlberg 2014; Giles et al. 2015; Dupret et al. 2017). Coelacanth endocasts are exceedingly rare. The shape of the cranial cavity housing the brain is only known in the extant genus, *Latimeria* (Millot and Anthony 1958) and one Devonian taxon *Diplocercides* (Stensiö 1963). The new Gogo coelacanth herein is the second fossil coelacanth for which the neurocranium is substantially known in 3D from which a cranial endocast can be generated.

Despite having been known to science for over 125 years, the spatial relationship between the brain and braincase in a related group, the lungfishes, was only recently described and quantified (Clement et al. 2015). Through the application of virtual microtomography and 3D rendering software, brain-neurocranial spatial information can be visualised and analysed, and used to aid interpretation of fossil endocasts. We herein present the recent "brain-warp"

neural reconstruction technique, as used on the Australian lungfish for both juvenile (Clement et al. 2016) and adult specimens (new data). Furthermore, we discuss how brain-endocranial spatial data changes through ontogeny, and how it can be used to help interpret endocasts of fossil sarcopterygians. Potential application and limitations of this technique for use on coelacanths and other taxa are discussed.

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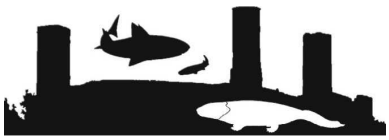

Examining the evolution and developmental mechanisms of oral odontode complexity in basal crown-group gnathostomes

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The origin of the different crown-gnathostome groups is associated with specialization in mineralized epithelial organs, called odontodes (Rücklin et al. 2011). Gene expression studies in chondrichthyans (cat-shark) and osteichthyans (cichlids) suggest that odontodes like teeth and denticles share a conserved gene regulatory network (GRN) with similar gene expression profiles (Fraser et al. 2009; Martin et al. 2016). Thus a major question is how does a fundamentally similar GRN generate the diversity of odontode structures seen amongst living and extinct jawed-vertebrates?

Here, we outline an approach, which integrates the fossil record of basal gnathostomes with a computational model of tooth development to examine the origins of oral odontode complexity. The main aims are to: (1) quantify the evolutionary patterns of oral odontode complexity in basal crown-group gnathostomes; and (2) use the *ToothMaker* platform (Salazar-Ciudad and Jernvall 2010) to simulate the observed disparity in oral odontode

complexity. We will use high-resolution micro-computed tomography to scan oral odontodes from fossil ganthostome groups spanning the split between chrondrichthyans and osteichthyans and use the generated surface models to measure surface complexity with the orientated patch count approach (Evans et al. 2007).

We expect a high degree of variability in oral odontode complexity between odontode classes (e.g., oral denticles, teeth) in the same jaw and across basal crown-gnathostome taxa as a whole. We hypothesise that by varying the synergism between signaling pathways and their interaction with tissue growth (i.e., Salazar-Ciudad and Jernvall 2004; Harjunmaa et al. 2012) it will be possible to generate different types of odontode complexity *in silico*.

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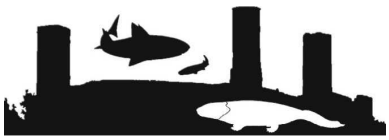

Articulated branchial skeletons in the "acanthodian" stem-chondrichthyans *Ptomacanthus anglicus* and *Diplacanthus crassissimus*

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The branchial arches of early gnathostomes provide a potentially rich source of morphological characters with which to understand jawed vertebrate evolution. However, due to the delicate

nature and arrangement of their component elements our understanding of their form in the gnathostome crown-group is limited almost entirely to crown-chondrichthyans and crown-osteichthyans. What information we do have from stem-group members of these clades is ambiguous either morphologically– eg. multiple conflicting interpretations of natural molds of the "acanthodian" stem-chondrichthyan *Acanthodes bronni* (Miles 1973; Gardiner 1984; Nelson 1968) – or phylogenetically – eg. the uncertain affinity of the putative stem-chondrichthyan *Ozarcus* (Pradel et al. 2014; Coates et al. 2017).

Here we considerably expand sampling of the chondrichthyan stem-group by using digital tomographic methods to visualise the branchial skeletons of two additional "acanthodians": the Early Devonian *Ptomacanthus anglicus* and the Middle Devonian *Diplacanthus crassissimus*. *Ptomacanthus* reveals an articulated branchial skeleton with five ventrally separated branchial arches, and a single basihyal that articulates with the hyoid arch and the first branchial arch. The branchial skeleton of *Diplacanthus* is less completely articulated, but preserves individual branchial elements in great detail and provides evidence for posteriorly directed pharyngobranchials. This provides morphologically and phylogenetically unambiguous data on the endoskeletal anatomy of two stem-chondrichthyans, and challenges recent hypotheses of the morphological evolution of the branchial skeleton in early gnathostomes (Pradel et al. 2014).

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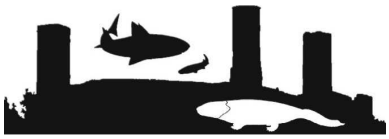

Predicting ectoparasitic pressure and grouping behavior in extinct early vertebrates from the study of their squamations.

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Grouping behavior involves some associated costs including the increase of the risk of parasite transmission (Richards *et al*., 2010). Some aspects of the squamation of sharks have been proposed as preventing factors for the settlement of ectoparasites (Ingram & Parker, 2006; Ferrón & Botella, 2017), however, there are no virtual works that specifically assess this question. Here, we have characterized the squamation of schooling sharks establishing a comparative framework for predicting ectoparasitic pressure and grouping behavior in extinct

early vertebrates with similar squamations. Scale coverage and crow angle have been analyzed in different body regions of 70 specimens of schooling and non-schooling sharks. Our results suggest that the squamation of sharks seems to respond to a trade off where hydrodynamic and protective functions prevail over defense against ectoparasites. A notable reduction in the scale density and an increase in crown angle are distinctive of schooling species that are not strong swimmers or benthic species living on hard substrates. Interestingly, similar patterns are characterized here in articulated specimens of the thelodont *Lanarkia horrida*. This suggests that social interactions (e.g. shoaling or schooling) could be present in vertebrates as early the Silurian and that ecotoparasitism could be an important selection pressure since very early stages in the evolution of the group.

This work has been founded by the Spanish Research Project CGL2014-52662-P and by the Generalitat Valenciana Research Project GV/2016/102.

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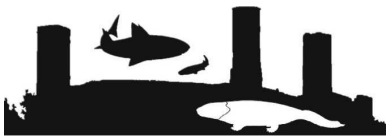

Ecological diversification patterns and diversity changes of thelodonts.

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Ecological diversification is a key topic in paleobiology. Up to date, only a few comprehensive studies dealing with this issue have been carried out in extinct groups of early vertebrates. Here, we explore the phylogenetic and spatial patterns of ecological diversification as well as the diversity changes of the whole clade of thelodonts, one of the earliest groups of vertebrates in the fossil record. For this, we have considered phylogenetic relationships proposed by Wilson & Märss (2004), the compilation of temporal and geographical occurrences provided by Märss *et al.*, (2007), the ecological data coming from scale functional morphology analyses (Ferrón & Botella, 2017) and sedimentological data (Turner, 1999).

Our results support that thelodonts originated in open waters of Laurasia, being a benthic lifestyle on hard substrates the ancestral condition for the whole group. Adaptations to fresh/brackish water, deep environments, fast swimming and schooling seem to have evolved independently in non-closely related groups and in different continents. In addition, diadromy

has possibly appeared also independently at least in nine different lineages. Some of the highest extinction rates of thelodonts coincide temporarily with other global or local Silurian extinction crises (e. g. Ireviken, Lau and Klonk events). Interestingly, diversity changes of demersal neritic species correlate with changes of sea level, several species of pelagic thelodonts adapted to strong swimming appeared during the Devonian coinciding with the so called Nekton Revolution, and species associated with deep-water habitats evolved during the Rhuddanian–Aeronian, coinciding with the lowest sea levels in the Silurian and with comparatively well-oxygenated outer continental shelves and upper continental slopes. In sum, this work reveals that thelodonts underwent a complex ecological diversification patterns and a high ecological diversity in terms of habitat and swimming capabilities, being comparable in some aspects to that of living condrichthyans and osteichthyans.

This work has been founded by the Spanish Research Project CGL2014-52662-P and by the Generalitat Valenciana Research Project GV/2016/102.

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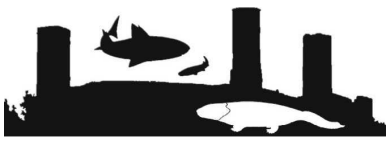

Skeletal remains of *Phoebodus politus* Newberry 1889 (Chondrichthyes: Elasmobranchii) from a Famennian Konservatlagerstätte in the eastern Anti-Atlas (Morocco) and its ecology

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The Devonian chondrichthyan *Phoebodus* (Newberry 1889) has long been known from isolated teeth recovered from a wide variety of fossil localities, ranging from the Middle Devonian to the Upper Missippian (Ginter *et al.* 2010). Here we provide a preliminary report of the first discovery of substantial, partly articulated skeletal and dental remains of a phoebodont, *Phoebodus politus*, from Famennian outrops of the eastern Anti-Atlas of Morocco.

Initial comparisons support the hypothesized close relationship of pheobodonts with the Upper Mississippian chondrichthyan *Thrinacodus gracia* (Grogan & Lund 2008, Ginter *et al.* 2010). Both taxa exhibit an anguiliform body and elongate slender cranium. However, *P.*

politus also exhibits dorsal fins with ctenacanth-like fin spines, echoing informal records of similar fin spine and tooth associations from the Famennian of Alaska (Maisey, *in* Ginter *et al*. 2010).

This Moroccan material represents an important addition to the limited data set of Devonian chondrichthyans. As such, these data will provide a valuable test of recent phylogenetic hypotheses (Pradel *et al*. 2011; Coates *et al*. 2017) and addition to analyses of early gathostome diversity and disparity before and after the end Devonian Hangenberg Event (Friedman & Sallan 2012).

Among living elasmobranchs, *Chlamydoselachus* uniquely displays a body shape, snout form and tooth morphology resembling those of *P. politus*. Acknowledging that the structure and likely biomechanics of the axial skeletons and jaws of these widey separated genera differ considerably, we nevertheless suggest that *Chlamydoselachus* (Ebert & Compagno 2009) provides the best available living model for understanding the ecomorphology of this remarkable, late Devonian comparator.

Coates, M. I., Gess, R. W., Finarelli, J. A., Criswell, K. E., & Tietjen, K. 2017. A symmoriiform chondrichthyan braincase and the origin of chimaeroid fishes. – *Nature*, **541(7636)**: 208-211.

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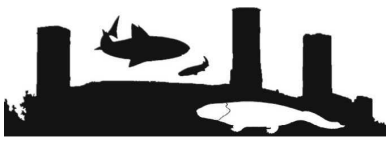

Estuarine fish breeding grounds: a comparison of the Famennian aged Waterloo Farm lagerstätten and contemporary systems

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The black Carbonaceous shales of the Famennian aged Witpoort Formation (Witteberg Group, Cape Supergroup) Waterloo Farm lagerstätten is interpreted as having been deposited in a quiet embayment of a back-barrier lagoonal estuary on the shores of the Agulhas Sea (Gess, 2016). Excavation of palaeontological material over several decades, including systematic collection of more than 500 vertebrate derived specimens, has provided a data base

from which ecological relationships can be extrapolated. Material includes both complete and incomplete growth series, providing an early example of the use of estuaries as fish nursaries. Evidence suggests that, as in recent estuaries (Whitfield, 1998) certain taxa (including both arthrodire and antiarch placoderms) spent their entire life cycle within the estuarine environment (eg. Gess and Trinajstic, 2017) whereas others (including the coelacanth, *Serenichthys*) only inhabited the estuary as juveniles and sub-adults (Gess and Coates, 2015 b). Sharks may have entered the estuary seasonally to feed and also to bear young (Gess and Coates, 2015 a). Additional taxa (including gyracanthid acanthodians) (Gess, 2016) are only evidenced by the dissociated remains of large adults that may have entered the estuary to feed on juvenile fish (or, in some cases, may have been washed in post mortem from adjacent more fresh-water environments).

Gess, R.W**.** 2016. Vertebrate biostratigraphy of the Witteberg Group and the Devonian Carboniferous boundary in South Africa. *In*: Linol, B. and M. J. de Wit (*Eds*), *The Origin and Evolution of the Cape Mountains and Karoo Basin,* pp. 131-140. Springer*, Regional Geology Reviews*. pp 131-140. Doi: 10.1007/978-3-319-40859-0_13

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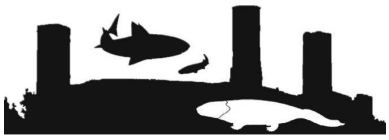

Reassessment of *Perleidus stoschiensis* from the Early Triassic of Greenland

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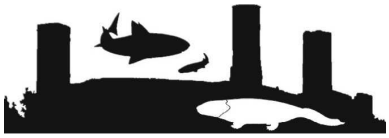
'Perleididae' is a widespread and speciose assemblage of ray-finned fishes spanning the Early to Late Triassic commonly affiliated with the neopterygian stem, although research conducted during the past 20 years has shed doubts on its monophyly. '*Perleidus' stoschiensis*, from the Early Triassic of East Greenland, is among the earliest and most comprehensively known 'perleidids', described from both dermal and endoskeletal material. Despite this, the limitations of traditional preparative and descriptive techniques have led to a poor understanding of much of the phylogenetically important internal skeletal anatomy, particularly the palate, gill skeleton and endocast. CT scanning of a near-articulated cranium permits detailed understanding of these regions, revealing primitive features such as a

basipterygoid fenestra in the palate, a fused dermohyal, and a lateral cranial canal with posterior connection only to the cranial cavity; as well as unusual characters such as a pronounced palatal dentition of blunt teeth, and a hyoid arch with three intermediary elements between the hyomandibula and ceratohyal. Discrepancies in braincase anatomy with previously described specimens of '*Perleidus' stoschiensis* hints at additional diversity within the genus. Inclusion within a new phylogenetic analysis places *'Perleidus' stoschiensis* on the actinopterygian stem, in contrast with previous resolutions as a crownward stem neopterygian. Such analyses also allow the recent suggestion that Early Triassic representatives of *Perleidus* be moved to a new genus, *Teffichthys*, to be tested in a phylogenetic framework.



Symmoriiform sharks from the Pennsylvanian of Nebraska

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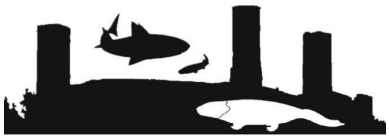
The Indian Cave Sandstone (Upper Pennsylvanian, Gzhelian) from the area of Peru, Nebraska, USA, yielded numerous isolated chondrichthyan remains and among them teeth and dermal denticles of the Symmoriiformes. Two tooth-based taxa were identified: a falcatid *Denaea saltsmani* Ginter & Hansen, 2010, and a new *Stethacanthus*-like form, with a peculiar, concave basolabial projection. In addition, there occur a few long, monocuspid tooth-like denticles, similar to those observed in *Cobelodus*, probably representing the head cover or the spine-brush complex.

Ginter, M. & Hansen, M. 2010. Teeth of the cladodont shark *Denaea* from the Carboniferous of central North America. – *In*: D. Nowakowski (*Ed.*), Morphology and systematics of fossil vertebrates, 29-44. DN Publisher; Wrocław.



Evolutionary lineages in the family Psammosteidae (Agnatha: Pteraspidiformes)

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Psammosteid heterostracans (suborder Psammosteida *sensu* Halstead Tarlo 1965) underwent the stages of assimilative (e.g. families Drepanaspididae, Obrucheviidae) and regressive (family Psammosteidae) phases of exoskeletal development during their evolution. The representatives of the family Psammosteidae *sensu* Novitskaya (2004) are characterized by

the slight exoskeleton, branchial plates are shortened (stenobasal) and stretched in width (l:w ≤ 0.6), median plates are full covered by tesserae (advanced tesserization), micromeric elements (tesserae and body scales) are small and with areal zones of growth (cyclomorial), in fields of tesserae are dominate single elements (odontodes) and simple complex elements, which may don't fuse in more large plates (tesserae etc.). Currently in the family Psammosteidae are included *Psammosteus* and provisorily retained *Karelosteus* (Novitskaya 2004, Glinskiy & Mark-Kurik 2016). The characters of the Psammosteidae first appear in *Tartuosteus* (?) *luhai* Mark-Kurik, 1965 (it need a new genus name) from the Middle Devonian (Givetian) of the Main Devonian Field. A phylogenetic analysis was carried out in order to determine the relative phylogenetic position of *T.* (?) *luhai*, in total 102 characters and 31 taxa of psammosteids were analyzed. In the result of the heuristic calculation in programm NONA 2.0 (algorithm Rathcet, 1000 interpretations), *T.* (?) *luhai* are placed in the same clade with *Psammosteus bergi* (Obruchev, 1943). *T.* (?) *luhai* should be considered a common ancestor of the *Psammosteus* species because its branchial plates still has a concave anterior part of median margin and dorsal plate is covered by small scale-like cyclomorial tesserae with eccentric position of primordial tubercles. In the appeared after *T.* (?) *luhai* members of *Psammosteus* (group of species from *P. bergi* to *P. megalopteryx* (Trautschold, 1880)) and also *Karelosteus weberi* Obruchev, 1933 are formed a full reduction of the anterior part of median margin of the branchial plates and cyclomorial, mostly polygonal concentric tesserae of the basic morpho-histological type (Glinskiy & Nilov 2017). It should be noted a group of species *"Psammosteus" ramosus* Glinskiy, 2017 - *"P". falcatus* Obruchev in Gross, 1942 from the Upper Devonian (Frasnian) of the Main Devonian Field, Scotland and Ellesmere Island. This psammosteids have extreme stenobasal branchial plates (l:w≤0.3) and discrete tesserae of the progressive morpho-histological type (odontode-like shape), which represent the circular stage of the tesserae development (Glinskiy & Nilov 2017).

Glinskiy, V. N. & Mark-Kurik, E. 2016. Revision of *Psammosteus livonicus* Obruchev (Agnatha, Heterostraci) from the Devonian Amata Regional Stage of the NW of the East European Platform. – *Estonian Journal of Earth Sciences*, **65** (1), 1-18.

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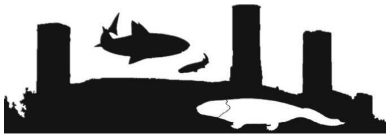
Novitskaya, L. I. 2004. Subclass Heterostraci. – *In*: L. I. Novitskaya and O. B Afanassieva (*Eds.*), *Fossil Vertebrates of Russia and Adjacent Countries. Agnathans and Early Fishes*, pp. 69-207. *Geos Press*, Moscow [in Russian].



Unexpected morphological convergence of the lateral line and caudal fin in a Paleogene teleost and sarcopterygian fishes

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The mechanosensory lateral line of teleost fishes is typically carried in a canal through a series of scales (discontinuous in some taxa) along each side of the body (DeLamater and Courtenay, 1973; Webb, 1989). While individual neuromasts do occur on the caudal fin of some teleosts (e.g. the Medaka, *Oryzias latipes*; Wada et al. 2008), the lateral line canal characteristically ends in the posterior-most lateral line scale at the base of the caudal peduncle and anterior to the caudal fin itself.

We note here a highly unusual configuration of the posterior portion of the lateral line in a large (~1.2m total length), nearly complete, and three-dimensionally preserved tarpon-like teleost (Elopomorpha, Megalopidae) from the Paleogene Red Bluff Tuff of Pitt Island (Chatham Islands), New Zealand. The specimen clearly shows a series of six progressively smaller lateral line scales that continue beyond the posterior border of the caudal peduncle and carry the lateral line canal over the medial caudal fin rays. These scales have attenuated posterior borders, rather than the straight vertical posterior borders of the lateral line scales anterior to the caudal fin. They are *in situ* and have not been displaced from elsewhere on the body, and the lateral line canal is clearly visible passing through these scales in cross-section where there is a break in the specimen. This configuration is convergently similar to the pattern in some tetrapodomorph and actinistian sarcopterygian fishes in which the lateral line extends onto the caudal fin via the squamation of an epicaudal lobe. The strongly developed caudal fin on the New Zealand megalopid is in other respects conventionally homocercal, with an externally symmetrical and deeply forked equilobate shape like that of a Recent tarpon.

The unique configuration noted here would likely have had significant mechanosensory implications, particularly considering that tarpons are active and powerful pursuit predators – assuming a similar lifestyle in the fossil tarpon, the lateral line mechanoreceptors on the caudal fin would have been subjected to substantial hydrodynamic stimulation, particularly during fast bursts of speed while pursuing prey. We further suggest that this unusual configuration is more like the arrangement of the comparable structures on some sarcopterygian fishes, and fundamentally different from what is seen with respect to caudally positioned neuromasts on Recent teleosts such as the Medaka, in which the terminal and accessory caudal neuromasts form earlier than the caudal fin and the scale rows, and then migrate into their final positions (Wada et al. 2008).

DeLamater, E.D. & Courtenay, W.R., Jr. 1973. Variations in structure of the lateral-line canal on scales of teleostean fishes. – *Zeitschrift für Morphologie der Tiere*, **75**: 259-266.

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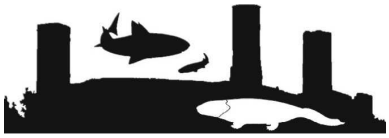
Webb, J.F. 1989. Gross morphology and evolution of the mechanoreceptive lateral-line system in teleost fishes. – *Brain, Behavior, and Evolution*, **33**: 34-43.



A Late Viséan (Early Carboniferous) chondrichthyan assemblage from a neptunian dyke of Rösenbeck (Rhenish Mountains, Germany)

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The Devonian reef limestone that is exposed in the Rösenbeck quarry near Brilon (Rhenish Mountains) shows numerous neptunian dykes and other hollows, which were filled with Carboniferous siliciclastic as well as fossil-rich blocks of carbonates. The carbonate sediments were deposited in elevated areas but subsequently eroded and transported as erratic blocks into the karstic cavities. Ammonoids, trilobites, numerous conodonts and chondrichthyan mircoremains demonstrate that two stratigraphic intervals are represented in the dyke sediments. Trilobite-rich carbonates from the Tournaisian-Viséan boundary interval and chondricthyan microfossils together with ammonoids and conodonts from the Late Viséan (Asbian-Brigantian) have been identified (Heuer et al. 2015).

The chondricthyan microremains can be attributed to various groups including the Symmoriiformes, Squatinactiformes, Phoebodontiformes and Holocephali. The teeth have been determined as belonging to *Denaea* cf. *fournieri*, *Thrinacodus* cf. *gracia*, ?*Squatinactis* sp. nov.; Holocephali gen. et sp. indet., Ctenacanthidae gen. et sp. indet., Elasmobranchii gen. et sp. indet. and Euselachii gen. et sp. indet. Associated with the teeth are dermal denticles, ctenacanth- and hybodont-type scales.

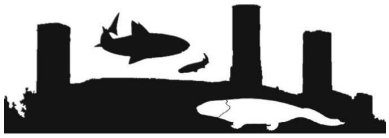
The teeth of ?*Squatinactis* sp. nov. have an arched base with two lingual buttons and two triangular basal projections; they are widely spaced by a deep depression below the central cusp. The crown is characterised by a central main cusp, up to six lateral cusps of subequal sizes on each side and numerous, densely packed labial cusplets in irregular rows; all these are inclined lingually. The cusps and the cusplets are ornamented with a few, but strong cristae which are usually more prominent on their labial side.

A large number of the falcatid teeth of cladodont morphology, assigned to *Denaea*, suggest a probable offshore assemblage. Other taxa would seem to be rare visitors to the waters covering the Rhenohercynian shelf as indicated by a very low amount of collected material. Similar but more diverse chondrichthyan assemblagesare already known from Late Viséan sediments of Poland, Germany and England (e.g. Ginter et al., 2010, 2015).

Ginter, M., Hampe, O. & Duffin, C. J. 2010. Chondrichthyes. Paleozoic Elasmobranchii: Teeth, in: Handbook of Paleoichthyology, edited by: Schultze, H.-P., Friedrich Pfeil, München, 168 pp.

Ginter, M., Duffin, C.J., Dean, M.T. & Korn, D. 2015. Late Viséan pelagic chondrichthyans from northern Europe. – *Acta Palaeontologica Polonica* **60** (4): 899–922.

Heuer, F., Korn, D., Belka, Z. & Hairapetian, V. 2015. Facies, origin, and palaeontological inventory of an Early Carboniferous neptunian dyke in the Devonian reef limestone near Rösenbeck (Brilon Anticline, Rhenish Mountains). – *Fossil Record*, **18**: 57-72.



Temporal niche separation in Arthrodires from the Gogo Formation, Western Australia

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Niche partitioning allows competing species to use the environment to facilitate their coexistence and is common in modern (Feer & Pincebourde, 2005; Helfman, 1986) and ancient (Motani, Rothschild, & Wahl Jr, 1999; Schmitz & Motani, 2011) ecological communities. The three-dimensionally preserved fish fauna of the Gogo Formation provide an ideal opportunity to determine if niche differentiation was present in the Canning Reef environments. Temporal niche separation allows species to operate in the same environment but at different times and may account for the biodiversity found amongst the Gogo fishes. Orbit size has been shown to be highly correlated with eye size which in turn is highly correlated to temporal period of activity (Schmitz & Wainwright, 2011). Thus by measuring the orbit size of vertebrates it is possible to infer their temporal niche and identify temporal niche separation between otherwise similar species whose behaviour is unable to be observed directly.

Qualitative assessments of the orbits of fossil fish from the Gogo formation have been suggestive of species-specific differences in eye size. Quantitative measurements of orbits and head length of five Gogo Arthrodire genera and two Dipnoan genera this have confirmed assessment. Eye size is species-specific. Ontogenetic growth series for *Compagopiscis* and *Griphognathus* show allometric growth indicating that there are no ontogenetic changes associated with eye size for these genera.

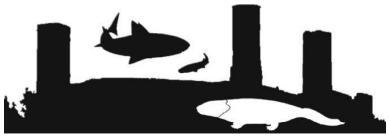
Feer, F., & Pincebourde, S. 2005. Diel flight activity and ecological segregation within an assemblage of tropical forest dung and carrion beetles. *Journal of Tropical Ecology*, *21*, 21–30.

Helfman, G. S. 1986. Fish behavior by day, night and twilight. *In* T. J. Pitcher (*Ed.*), *The Behaviour of Teleost Fishes* (pp. 479–512). Springer.

Motani, R., Rothschild, B. M., & Wahl Jr, W. 1999. Large eyeballs in diving ichthyosaurs. *Nature*, **402**(1998), 747.

Schmitz, L., & Motani, R. 2011. Nocturnality in dinosaurs inferred from scleral ring and orbit morphology. *Science*, **332**, 705–708.

Schmitz, L., & Wainwright, P. C. (2011). Nocturnality constrains morphological and functional diversity in the eyes of reef fishes. *BMC Evolutionary Biology*, **11**(1), 338.



An Articulated Dentition of *Psephodus* from the Lower Carboniferous (Viséan) of Indiana, USA

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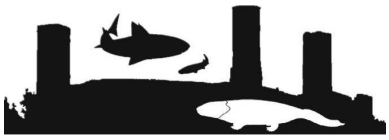
Psephodus is a cochliodontiform fish, whose dentition consists of a few large rectangular or rhomboidal tooth plates and numerous smaller oblong tooth plates. Up to three plates have been found in an articulated series (Davis, 1883). Recently, a partial dentition of *Psephodus* was collected from the Big Clifty Formation of Crawford County, Indiana, USA. The Big Clifty Formation lies within Zone V3cs of the type Viséan sequence in Belgium. The new specimen comprises four tooth plates belonging to a single ramus. They fit closely together and are in their original positions with respect to each other. Whether the plates belong to the lower or the upper dentition is not known. The plates lie in a sequence, with the largest plate being the most distal and the smallest being the most mesial. The most distal plate, which is rhomboidal and mesio-distally elongated, is very much larger than the other three plates, which are oblong and labio-lingually elongated. The mesio-distal and labio-lingual dimensions of the rhomboidal plate are 23 mm and 15.5 mm, respectively. The corresponding dimensions of the adjacent oblong plate are 3.0 mm and 8.0 mm, respectively. The mesio-distal dimension of the entire series is 33 mm. The large plate of the new specimen resembles the holotype of *Psephodus regularis*, also from the Viséan of Indiana. However, the new specimen is considerably more convex than the holotype and may represent a component of the opposing dentition. The new specimen invalidates the reconstruction of the *Psephodus* dentition of Davis (1883), who placed three large plates in the ramus of each jaw. It also invalidates the reconstruction of St. John and Worthen (1883), who placed a single large plate on each ramus, flanked by families of small teeth on both mesial and distal sides. The reconstruction of Branson (1905), with only three tooth plates on each ramus, is also ruled out. Traquair (1885) described a set of associated but disarticulated tooth plates of *Psephodus magnus* and many, small *Helodus*-like teeth that he presumed to be from the same individual. The presence of additional, small, anterior teeth in the dentition of *Psephodus* is not ruled out by the new specimen, but there does not seem to be room for all of the 44 small teeth seen in the specimen described by Traquair. That specimen might represent the remains of more than one individual or of more than one species. Zangerl (1981, figs. 18C,D) reconstructed the *Psephodus* dentition with tooth plates lined up in replacement files, smaller plates being positioned **lingually** of the larger plates. This reconstruction might have been based on a misinterpretation of an associated set of *Psephodus* tooth plates, like the one described here, as a tooth **family**. Such an arrangement would imply either that replacement plates continued to grow, once formed, or that replacement took place in a **labial** to **lingual** direction.

Branson, E.B. 1905. Notes on some Carboniferous cochliodonts with descriptions of seven new species. – *Journal of Geology* **13** (1): 20-34.

Davis, J.W. 1883. On the fossil fishes of the Carboniferous Limestone Series. – *Scientific Transactions of the Royal Dublin Society* **1**: 327-548.

St. John, O. & Worthen, A.H. 1883. Descriptions of fossil fishes. – *Geological Survey of Illinois* **7**: 55-264.
Traquair, R.H. 1885. On a Specimen of *Psephodus magnus*, Agassiz, from the Carboniferous Limestone of East Kilbride, Lanarkshire. – *Geological Magazine* **2** (8): 337-344.
Zangerl, R. 1981. Chondrichthyes I: Paleozoic elasmobranchii. *In*: H.-P. Schultze (ed.), *Handbook of Paleoichthyology* **3A**: 1-115. Gustav Fischer Verlag, Stuttgart, Germany.



New chondrichthyans from the Late Carboniferous of European Russia.

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The diverse chondrichthyan assemblages were recorded from the Kasimovian and Gzhelian (Late Carboniferous) of two regions in the East European Platform: Moscow and Samara regions. The chondrichthyan remains, including the teeth of symmoriiform *Stethacanthus* sp.; xenacanthoid *Bransonella nebraskensis* (Johnson); ctenacanthiform *Heslerodus divergens* (Trautschold); jalodontid *Adamantina foliacea* Ivanov; a new genus of euselachian; neoselachians *Cooleyella amazonensis* Duffin, Richter and Neis and *C.* sp.; a new peculiar elasmobranch; as well as various scales, were found in the key sections of Kasimovian and Gzhelian (Rusavkino and Gzhel) of Moscow Region.

The Kasimovian and Gzhelian deposits of Samarskaya Luka, Volga River Basin (Samara Region) yielded the teeth of symmoriiforms *Denae wangi* Wang, Jin and Wang and *Denae* sp., ctenacanthiforms *Heslerodus divergens* (Trautschold) and *Glikmanius sp.;* jalodontid *Adamantina foliacea* Ivanov, a new genus of euselachian, a new peculiar elasmobranch; helodontiforms, cochliodontiforms, and numerous denticles.

A new genus of euselachian is characterized by a pyramidal crown with labial and lingual rows of well-developed serrated projections. These teeth resemble the teeth of *Deihim* (Ginter et al. 2002) and *Tiaraju* (Richter 2007) but the projections in the crown of new taxon were strongly extended on both tooth sides.

The teeth of a new peculiar elasmobranch possess the phoebodont crown with three well-separated, equal cusps and triangular base with two small labio-basal tubercles. The cusps are considerably sigmoidally curved and mesio-distally widened in the upper part. The lateral carina is present only in the widened upper part of the cusp. The labial surface of the cusps is smooth but the lingual side bears the numerous distinct cristae. The cusps are built of orthodentine. The internal vascularization system of the tooth base is composed of three large transversal and short ascending canals. These teeth are distinguished from the teeth of all known Paleozoic chondrichthyans. But they are similar in the cusp design to a tooth recently described as Falcatidae indet. from the Early Cretaceous of France (Guinot et al. 2013). The Cretaceous tooth has a cladodont crown and a base missing the labio-basal tubercles. Possibly this new taxon from the Late Carboniferous is an oldest representative of those Mesozoic sharks.

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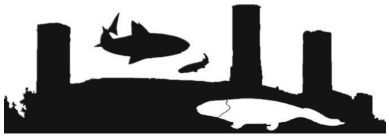

Internal structure of the Paleozoic "chondrichthyan" scales

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The internal structure of isolated scales of different morphogenetic types in the Paleozoic chondrichthyans and some fishes questionable attributing to chondrichthyans was studied utilizing the micro-CT Bruker SkyScan 1172 with visualization software.

The scale of *Cladolepis* from the Givetian, Middle Devonian of Kuznetsk Basin (Russia) is growing, polyodontodia type. The crown contains the odontodes placed at the different distance from each other and surrounded by foramina of vascular canals. The horizontal canals and their ramifications is formed the network located in the crown especially in the posterior part. This network is connected to the small pulp canals of the odontodes by short ascending canals.

The scales of *Karksilepis* from the Givetian (Middle Devonian) of Estonia are polyodontodia type with non-growing base, have the long separated odontodes and the base composed of lamellar tissue with bone cell lacunae. The canal system in the scale base includes the undulated main horizontal canals with numerous ramifications and ascending short canals penetrating the base. The pulp canals of odontodes are connected with some horizontal canals.

The non-growing scale of *Mongolepis* from the Llandovery (Silurian) of Mongolia possess the very compound odontocomplex in the crown and flat base bearing the numerous large foramina. The odontocomplex consists of small odontodes arranged in parallel rows. The pulp canals of odontodes in the row are connected by horizontal canals. The large vertical canals in the scale base run to the canal network of the crown.

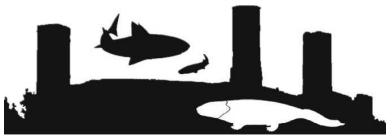
The orodontid scale from the Serpukhovian (Early Carboniferous) of Moscow Region is growing with compact odontocomplex in the crown. The central primordial odontode is surrounded the elongated additional odontodes. The numerous foramina of canals open on the lateral and posterior sides of the scale neck. The rows of foramina are placed on the boundary between the odontodes. The network of vascular canals consists of the meandering horizontal and ascending basal canals, and the branched neck canals.

The most complicate system of vascular canals is observed in the regularly growing polyodontode scales of ctenacanthid type from the Serpukhovian (Early Carboniferous) of Moscow Region. The most part of odontode is composed of osteodentine. The foramina of

canals open in the anterior surface of the neck and base but the large foramina are penetrated the posterior surface of the neck. The compound network of canals are occupied the entire scale. The ascending canals run from the basal side through the neck to each odontode. These canals are connected each other by short horizontal or inclined ramifications. The neck canals are formed the dense network with the ascending canals in the lower part of the crown.

The euselachian scale from the Sakmarian (Early Permian) of the South Urals possesses the simplified canal system. The ascending canals run from the base to the crown and pass into the large, pulp cavities. The short horizontal neck canals are connected with the ascending canals. Such scales probably belong to non-growing type.

The study was partly supported by a grant from Saint-Petersburg State University No. 0.38.292.2015 and performed at the Center for Geo-Environmental Research and Modeling (GEOMODEL) of Research park of St. Petersburg State University.



The first tristichopterid tetrapodomorph from the upper Frasnian of the Holy Cross Mountains, Poland

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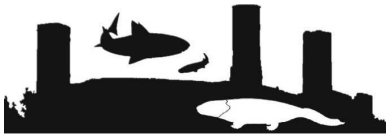
Late Devonian osteichthyans form the Holy Cross Mountains occur rarely and are known poorly. The only papers, which report sarcopterygians discuss the occurrences of dipnoans (Gorizdro-Kulczycka, 1950, but see also Skrzycki et al. in this volume) and actinistian (Szrek, 2007). We repot here the first occurrence of the of Tristichopterida in the uppermost Frasnian of the Wietrznia Quarry in the Holy Cross Mts.

Remains are represented by the fragments of lower and upper jaw. They belonged to the small individual, which head does not extend 3,5 cm in length. The material is incomplete but allows to identify it as the most similar to *Medoevia lata* (Lebedev, 1995). However, *M. lata* is typically much bigger, and in age and slightly younger. Polish specimens are late Frasnian (based on conodonts) while *M. lata* is probably late Famennian. Therefore a form from the Holy Cross Mountains may represent a new species of this genus or a new genus within tristichopterids.

Gorizdro-Kulczycka, Z. 1950. Les Dipneustes dévoniens du Massif de S-te Croix. *Acta Geologica Polonica*, **1**: 53-105.

Lebedev, O. 1995. Morphology of a new osteolepidid fish from Russia. Bulletin du Museum National d'Histoire Naturelle,Paris, 17: 287-341.

Szrek, P. 2007. Coelacanths (Actinistia, Sarcopterygii) from the Famennian (Upper Devonian) of Kadzielnia Chain, Holy Cross Mountains, Poland. *Acta Geologica Polonica*, **57**: 403-413.



Fusion in the vertebral column of the pachyosteomorph arthrodire *Dunkleosteus terrelli* ('Placodermi')

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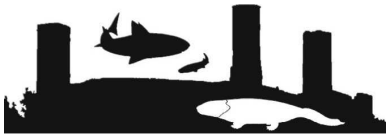
Fusion in the vertebral column occurs normally in jawed vertebrates, with structures like the sacrum and pygostyle providing rigidity, support and increased area for muscle attachment. The synarcual represents the fusion of the anterior part of the vertebral column and occurs in a number of jawed vertebrates, including a variety of placoderms and chondrichthyans. Placoderms are an entirely fossil group of armoured fishes (Silurian-Devonian), resolved to the base of the jawed vertebrate clade, with vertebrae comprising neural and haemal arches composed of perichondral bone. The placoderm synarcual preserves substantial developmental information from anterior (oldest) to posterior, where new vertebrae are incorporated.

A subadult specimen of the pachyosteomorph arthrodire *Dunkleosteus terrellli* preserves vertebral elements showing varying degrees of anteroposterior fusion along the vertebral column. Synarcuals are rarely preserved in this group, and micro-CT scanning of this synarcual provides details of a transitional zone of vertebral fusion, providing unprecedented information on how each vertebrae is modified and incorporated into the synarcual. All elements in the synarcual retain vertebral identity, showing less fusion overall, more comparable to other arthrodires such as *Compagopiscis*. By comparison, synarcuals of other taxa such as ptyctodont placoderms, batoids, holocephalans (Chondrichthyes) and mammals (syncervical) show more complete fusion of vertebral elements.



Orthacanthus platypternus (Chondrichthyes: Xenacanthiformes) teeth and other sharks and microvertebrate remains from the Lower Permian Craddock Bonebed, lower Clear Fork Group, Texas, USA

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An unusual 6-8 cm layer of prismatic cartilage and matrix containing teeth, incomplete occipital spines, and denticles of *Orthacanthus platypternus* occurs in the Craddock Bonebed, best known for producing amphibians and reptiles. Approximately two m2 of this layer was sampled as nine contiguous areas (IIX). These were screen-washed and some fractions were treated with ≤ 10% acetic acid. Some 8800 recovered teeth from three of the areas (I, III, V) demonstrate that *O. platypternus* is the only species of shark present except for several worn *Xenacanthus* occipital spine fragments and two teeth of ?*Lissodus* (*Polyacrodus*) *zideki* (Hybodontoidei), both first occurrences in the Clear Fork.

Measurements of *O. platypternus* teeth with complete bases (anteromedial-posterolateral or am-pl length, labial-lingual or l-l width) were randomly selected from 3050 initially available teeth in Areas I, III, and V. Nearly all of the teeth have broken cusps, making it difficult to determine their position in the dental arcade without knowing the attitude of the principal cusps (posterior teeth are more easily recognized because of their small size and tendency to lack the intermediate cusp). In each case, larger teeth (A; retained on ≥20 mesh screens) were kept segregated from smaller teeth (B; retained on ≤30 mesh screens). The smaller fractions were assumed to be dominated by juveniles; an independent study has identified the presence of juvenile occipital spines. Linear regression analysis (y = mx + b; x = ampl, y = l-l) of the dimensions reveals that the small fractions (B) have a lower slope (m) than the larger fractions (A) (means and ranges for Area I serve as an example): Area IA (n =100), y = 0.71x + 0.22, xm = 2.54 mm (1.10—8.63 mm), ym = 2.02 mm (0.96—6.35 mm); Area IB (n = 30), y = 0.51x + 0.45, xm = 1.04 mm (0.78—1.36 mm), ym = 0.99 mm (0.72—1.20 mm); Area IIIA (n = 69), y = 0.69x + 0.32; Area IIIB (n = 20), y = 0.40x + 0.60; Area VA (n = 99), y = 0.72x + 0.30; and Area VB (n = 25), y = 0.48x + 0.46. This analysis failed to reveal the presence of sexual dimorphism or the presence of juveniles as clusters in the scatter diagrams, unlike studies of the occipital spines. Tooth analyses in other faunas at about the same stratigraphic level have similar values.

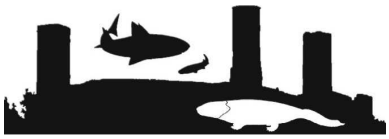
Other specific morphological features are unknown. One possible exception is the presence of a few highly symmetrical small teeth with vertical or slightly divergent principal cusps and antero-posterior base length much greater than the labiallingual width. Such teeth have not been previously observed in the Clear Fork Group or underlying Wichita Group. They may be symphyseals and restricted only to juveniles. Other unusual teeth include germinal teeth and deformed teeth, both of which occur in the Wichita and Clear Fork groups. Germinal teeth have a normal base, but the principal cusps are only partly developed, and usually the intermediate cusp is undeveloped. They constitute 2 .% of the tooth sample. Deformed teeth may have “knob-like” principal cusps, which may be partly fused, or the intermediate cusp is replaced by a ridge, or the apical button is absent or distorted in various

ways, as well as other forms of distortion. Nevertheless, they are rare, as in other faunas, amounting to 0.6% of the total number of teeth.

Perhaps the most unusual teeth, in that they had not been specifically observed in other faunas in the Clear Fork Group, are those that appear to have undergone various stages of resorption. They represent nearly 6% of the total sample. Only the lingual margin of the base is affected. Some merely have an etched margin, but in others the apical button is resorbed to varying degrees until only the labial margin with the basal tubercle and the three cusps are all that remain. In a typical tooth file, the basal tubercle rests upon the apical button of the preceding tooth. If the teeth were undergoing resorption, then the perplexing problem is why the apical button is resorbed and not the superjacent basal tubercle. Some other, but unknown, pathological process may have been occurring.

One tooth, obviously pathologically deformed, displays an apparent example of the equivalent of an "enamel pearl" on one of its cusps, although enamel and enameloid are absent. This may be the only known occurrence of this condition from the Lower Permian.

Other microvertebrates include *O. platypternus* tooth fragments and cusps, cartilage fragments, and coprolites. Also present are palaeoniscoid scales and teeth and unidentified tetrapod bone fragments, jaw fragments, and teeth. Rare fragments of bones (scales?) bear a "comb edge" which have not been previously observed in the Texas Lower Permian. Another rare occurrence includes *Diplocaulus*? bone fragments.



Life history of the stem tetrapod *Hyneria lindae*

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[2] Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA.
[3] European Synchrotron Radiation Facility, Grenoble, France.
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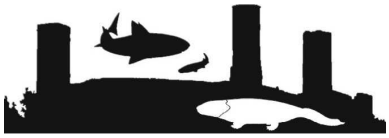
Recently, attempts have been made to utilize limb-bone histology as a source of data for understanding the ecological dimension of the fin-limb transition. Here we present histological life history data from a humerus (ANSP 21483) of *Hyneria lindae*, a finned member of the tetrapod stem group from the Late Devonian Catskill Formation (Pennsylvania, USA), obtained by propagation phase contrast synchrotron microtomography (ESRF, France). The humerus of *Hyneria* is made of a large spongiosa surrounded by a slightly vascularised compact cortical bone. This is similar to the humeral histology of *Eusthenopteron foordi* and the limbed stem tetrapod *Acanthostega gunnari*, with a spongiosa containing primitive bone marrow processes, indicating that bone marrow was already intimately associated with long-bone elongation and endochondral ossification before the transition from fins to limbs. The humerus presents a mixture of 'juvenile' and 'adult' histological features, suggesting either that it represents a subadult individual or that *Hyneria lindae* was in some respects paedomorphic. The latter hypothesis is supported by the unossified condition of the endocranium even in large individuals. The thin humeral cortex

exhibits a relatively slow bone growth rate. Interestingly, *Eusthenopteron foordi* and *Acanthostega gunnari* also show slow growth and late (> 6 years) sexual maturity. A broad-sample investigation of additional taxa will be needed to assess the generality of this pattern and map the reproductive trends during the early evolution of the tetrapod stem.



A second skull of "*Ligulalepis*"

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Previously, a single specimen of an isolated osteichthyan skull and braincase, referred to the genus "*Ligulalepis*", was known from the Emsian Wee Jasper limestones in New South Wales, Australia. The specimen has been interpreted either as a stem osteichthyan (Basden et al. 2000) or a stem actinopterygian (Basden and Young 2001). However, this first specimen was anteriorly incomplete, obscuring details of the skull roof and nasal capsules.

Here we describe a second specimen, which preserves the previously unknown anterior region. Two newly described characters are shared with some early actinopterygians: the posterior nostril opens within the orbit, and the profile of the skull roof shows a distinct downturn (or "roman nose"). In addition, CT scans clarify details of the endocranial anatomy, and reveal an unusual line of pores lateral to the supraorbital sensory canal. Phylogenetic analysis remains ambiguous as to the placement of "*Ligulalepis*": stem osteichthyan, stem sarcopterygian, or stem actinopterygian placements are all plausible. "*Ligulalepis*" cannot be considered in isolation as the polarisation of key characters depends in part on the phylogenetic position of other basal osteichthyans: in particular the position of early Chinese taxa (such as *Guiyu, Psarolepis, Meemannia* etc.).

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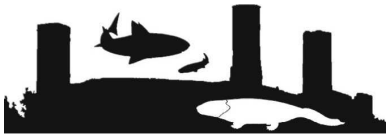
Basden, A. M. & Young, G. C. 2001. A primitive actinopterygian neurocranium from the Early Devonian of southeastern Australia. – *Journal of Vertebrate Paleontology* 21: 754-766.



Origin of the Konservatlagerstätten of the southern Maïder (Morocco) and gnathostome preservation

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In the Famennian of the eastern Anti-Atlas, microremains of gnathostomes are quite common in some strata due to condensed sedimentation, particularly in the Tafilalt. In the latter region, chondrichthyan diversity can be reasonably high (up to nine species in one layer). By contrast, in the Famennian of the southern Maïder Basin, chondrichthyan diversity appears to be lower (four to five species) and genera such as *Clairina*, *Jalodus* and *Protacrodus* have not been found yet although they are documented from the neighboring Tafilalt Basin (Ginter et al. 2002; Derycke et al. 2008).

We address the questions for the ecological factors controlling these differences in diversity and fossil preservation. The latter question is of interest because only in the Maïder Basin, chondrichthyans have been discovered preserving cartilaginous body parts as well as soft tissues.

Preservation has been examined by analyzing the mineral composition of various Famennian fossils from the Maïder and the Tafilalt using XRD (X-ray Diffraction) at the Swiss Federal Institute of Technology in Zurich (ETHZ). The results show that indeed the chondrichthyan musculature is now preserved in hematite and other ferric minerals. Both placoderm bones and chondrichthyan cartilage are preserved in hydroxylapatite, fluorapatite or francolite (phosphates). Particularly the abundance of ferric oxides and hydroxides points at pyrite, which was altered due to deep weathering in the desert environment. This is corroborated by rare finds of pyritized fossils from the same strata in depths of over 10 m below today's surface.

In turn, this primary abundance of pyrite (now ferric oxides and hydroxides) in combination with the clayey facies and the scarcity of benthos in some strata suggests that the sediments containing exceptionally preserved gnathostomes were deposited under oxygen-poor conditions (Klug et al. 2016). This is supported by the palaeogeographical situation of the Maïder Basin that was closed to the south, west and north by land, while to the east, the shallower regions of the Tafilalt Pelagic Ridge limited water exchange (Wendt 1988; Kaufmann 1998).

Hypoxic to anoxic conditions ultimately explain the absence of the protacrodontids, which mainly occur in shallower, better oxygenated waters (Ginter 2000). *Clairina* and *Jalodus* on the other hand likely preferred deeper environments than the one in the Maïder Basin. Following Ginter (2000), the taxa present in the Maïder (*Phoebodus* and cladodonts) point at an intermediate water depth.

Derycke, C., Spalletta, C., Perri, M. C. & Corradini, C. 2008. Famennian chondrichthyan microremains from Morocco and Sardinia. – *Journal of Paleontology*, **82**: 984-995.
Ginter, M. 2000. Late Famennian pelagic shark assemblages. – *Acta Geologica Polonica*, **50**: 369-386.

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Klug, C., Frey, L., Korn, D., Jattiot, R. & Rücklin, M. 2016. The oldest Gondwanan cephalopod mandibles (Hangenberg Black Shale, Late Devonian) and the Mid-Palaeozoic rise of jaws. – *Palaeontology*, **59**: 611-629. doi: 10.1111/pala.12248

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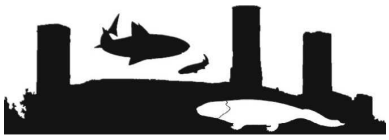

Paleozoogeographic implications of the new finds of enigmatic Late Devonian porolepiform *Ventalepis*

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In 1980 H.-P. Schultze described a new porolepiform species *Ventalepis ketleriensis* upon unusual scales and cranial elements from the Upper Famennian Ketleri locality in western Latvia. In 1999 new materials on this species were collected by one of the authors (O.L.) in the almost coeval deposits in Central Russia (Orel Region) (Lebedev & Lukševičs 2016). New studies in the type locality during the 2014-2016 field seasons also brought some additional elements. In 2016 O.L. discovered new *Ventalepis* evidence in the Upper Famennian Lnyanaya Formation (Novgorod Region, Russia) among other fish remains belonging to the same vertebrate assemblage.

The parieto-intertemporal and praeopercular unknown earlier are described; the scales are shown to belong to the rhomboid type. This bizarre fish differs from the members of the porolepiform families Porolepididae and Holoptychiidae by thick two-layered scales and minute denticulation over the non-overlapped surface of scales and bones. These cusps demonstrate the primitive condition among other types of ornamenting dermal denticles being similar to marginal teeth on the jaws or shagreen denticles on the dermal bones and platelets of the oral and branchial cavities by their conical shape, simple dentine folding at the base and simple conical pulp cavity. Unique features intrinsic to *Ventalepis* make us establish a new family for this taxon.

Abundant materials on *Ventalepis* scales made possible to pick up the specimens bearing lifetime traces of parasites. These traces first described by Lukševičs & al. (2009) look like small pits forming groups on the boundary between the overlapped and non-overlapped surfaces and might be produced by parasitic copepods (?).

Faunistic analysis performed by the authors (Lebedev & Lukševičs 2016) suggested *Ventalepis* to be a distinguishing member of the Ventalepis vertebrate community. New finds of this fish within the paleozoogeographic province of Baltica extend the zoogeographic area of this community, which occupied a vast territory in the northern and central part of the East European platform being confined to the coastal-marine territories and coastal lowlands periodically invaded by sea. Despite the dominance of local and provincial endemics in this

fauna (Lebedev & al. 2010), the zoogeographic analysis suggests the relationships of the community to the vertebrate faunas in East Greenland and Belgium.

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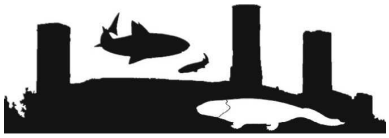
Schultze, H.-P. 1980. Crossopterygier-Schuppen aus dem obersten Oberdevon Lettlands (Osteichthyes, Pisces). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **4**, 215–228.



Fossil chondrichthyan and placoderm remains from the Middle Devonian South Blue Range, Victoria, Australia: biostratigraphic implications

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Fossil fishes were first discovered in the South Blue Range (SBR), near Mansfield, in the mid 1930s, and described by Hills (1936). First thought by Hills to be Late Devonian, later studies on the placoderms suggested the deposit to be older, probably Givetian in age. This site has yielded the placoderms *Bothriolepis* sp., *Austrophyllolepis edwini*, and *Groendlandaspis* sp. (Long 1989) plus the stem tetrapod fish *Owensia chooi* (Holland 2009). Chondrichthyan teeth are here described from a new site located in the upper section of the Middle Devonian Kevington Creek Formation in the South Blue Range, near Mansfield, Victoria (Cas *et al*. 2003). The teeth include a new species of *McMurdodus* with coarse serrations, supporting a possible late Eifelian-early Givetian age for the unit, as this genus is otherwise known only from the early Middle Devonian Cravens Peak beds of central Australia (Turner & Young 1987, Emsian-Eifelian boundary) and from the lowermost units of the Aztec Silstone (Givetian-Eifelian) in Antarctica. Other chondrichthyan taxa in the same fauna include *Aztecodus* sp. and *Antarctilamna prisca*, also known from the Aztec Siltstone fauna of Antarctica (Young 1982; Long & Young 1995). Remains of the antiarchs *Bothriolepis* sp. and ?*Venezuelepis* are consistent with this being a faunal assemblage with a wider Gondwanan aspect.

The younger occurrence of the genus *McMurdodus* in the Aztec Siltstone of Antarctica (Eifelian-Givetian) and the presence of *Aztecodus* sp. and *Antarctilamna* sp. in the Kevington Creek fauna would also support an older age for the whole South Blue Range Devonian succession. This implies the unconformity between the Devonian succession demarcated by the Mt. Kent Conglomerate (conformable with the Early Carboniferous Devils Plain Formation) could be chronologically longer than previously estimated.

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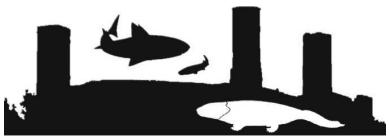
Long, J.A. 1989. Phyllolepid placoderm fishes from the Late Devonian of eastern Victoria. – *In*: R. Le Maitre (*Ed.*), *Pathways in Geology,* pp. 52-58. E.S. Hills Memorial Volume, *Blackwell Press*, Melbourne.

Long, J.A. & Young, G.C. 1995. New sharks from the Middle-Late Devonian Aztec Siltstone, southern Victoria Land, Antarctica. – *Records of the Western Australian Museum*, **17**: 287-308.

Turner, S. & Young, G.C. 1987. Shark teeth from the early-middle Devonian Cravens Peak Beds Georgina Basin. – *Alcheringa*, **11**: 233-244.



New information on the stem tetrapod group Canowindridae, based on synchrotron studies of *Koharolepis* from the Middle Devonian of Antarctica

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The evolution from water to land represents one of the greatest vertebrate evolutionary transitions, and much of our knowledge comes form study of the tetrapodomorph fishes (Osteichthyes: Sarcopterygii) which form the stem to the Tetrapoda.. Debate continues around the timing of this evolutionary step, and also whether the stem tetrapods first emerged in either the Northern or Southern Hemisphere, with the currently oldest representative sof the lineage found in China (Lu et al. 2012). Within various phylogenies the Canowindridae (comprising *Canowindra, Beelarongia* and *Koharolepis*) emerge as clade of basal stem tetrapods just crownward of rhizodontids and basal Chinese forms like *Tungsenia* and *Kenichthys*. They are characterised by having broad, flat skulls with triangular wide extratemoporal bones, lacking clear sutures between certain postparietal dermal bones, very small eyes, and some bear expanded cheek plates with additional postorbital bones.

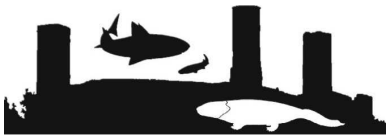
With the aid of the Australian synchrotron we herein present new imagining data using Mimics and Drishti on a key Gondwanan taxa, *Koharalepis jarviki* Young, Long & Ritchie1992 from the Middle Devonian Aztec Siltstone of Antarctica. The new CT data shows the presence of the braincase and articulated hyomandibula, some of the gill-arches and elucidates aspects of the lower jaw morphology. A new canowidridoid which we are currently describing from the Harajicca Sandstone, Northern Territory (see abstract by Choo et al, this volume), also shows details of parasphenoid and palate anatomy. All these data combine to build a clearer concept of the anatomy and functional morphology of the canowindrids, which appear to occupy a niche similar to glyptolepid porolepiforms in most East Gondwana Middle-Late Devonian faunas.

Revised phylogenetic relationships of stem tetrapods using Bayesian techniques shows that the enigmatic taxon *Marsdenichthys* Long 1985, first thought to be a basal tristichopterid, is now regarded as a possible sister taxon to other canowindridoids, making this set of taxa an endemic clade of East Gondwana stem tetrapods.

Long, J.A. 1985. The structure and relationships of a new osteolepiform fish from the Late Devonian of Victoria, Australia. – *Alcheringa*, **9**: 1-22.

Lu, J., Zhu, M., Long, J. A., Zhao, W., Senden, T. J., Jia, L. T. & Qiao, T. 2012. The earliest known stem-tetrapod from the Lower Devonian of China. – *Nature Communications,* **3:** 1160.

Young, G.C., Long, J.A. & Ritchie A. 1992. Crossopterygian fishes from the Devonian Aztec Siltstone, Antarctica**:** systematics, relationships and biogeographic significance. – *Records of the Australian Museum*, Supplement **14**: 1-77.



Tetrapodomorph fish from the Early-Middle Devonian of Australia shed light on the early evolution of stem-tetrapods

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Tetrapodomorpha, comprising all limbed vertebrates (tetrapods, such as frog, reptiles, birds and mammals) and their fish ancestors, have a fossil record back to the Early Devonian. Only two Early Devonian tetrapodomorph fishes have been reported, *Tungsenia* from the Pragian and *Kenichthys* from the Emsian (Chang and Zhu, 1993; Lu et al., 2012; Zhu and Ahlberg, 2004), both from South China and share many similarities with basal dipnomorphs, the sister group to tetrapodomorphs. Other Devonian tetrapodomorph fishes mainly occur in younger strata (Givetian - Famennian), and are highly specialized comparable to Early Devonian taxa, which leave a significant morphological and geological gap between them.

Here we clarify the morphology of a new genus of tetrapodomorph fish, from the Hatchery Creek group of Southeast Australia, originally described as '*Gyroptychius? australis*' on the skull roof features (Young and Gorter, 1981). A revised age suggests it may be late Emsian rather than Middle Devonian (Hunt and Young, 2012). In 2007, some skulls of '*Gyroptychius? australis*' were mechanically prepared at IVPP, Beijing and were CT scanned at ANU. The new anatomical information, particularly braincase morphology, reveals that the form is similar to Chinese basal tetrapodomorphs (e.g. *Tungsenia*, *Kenichthys* and *Thursius wudingensis*) in the posteriorly elongate parasphenoid which covers the whole notochordal facet. The broad tectum orbital in the ethmosphenoid region and the absence of the vestibular fontanelle in the otoccipital region recall the more primitive condition in *Styloichthys*, the onychodont *Qingmenodus* and coelacanths as well.

The new form fills the transitional gap between the primitive tetrapodomorph representatives and the typical 'osteolepids'. It helps us have a better understanding of the early evolution of the tetrapod lineage.

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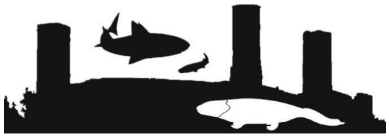
Zhu, M. & Ahlberg, P.E., 2004. The origin of the internal nostril of tetrapods. – *Nature*, **432**: 94–97.



Squamation of the Devonian asterolepid antiarchs: new data

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The squamous part of the trunk and tail is described in several antiarchs, mostly representatives of Asterolepiformes, including the Middle Devonian *Pterichthyodes* from Scotland (Hemmings 1978) and *Asterolepis ornata* Eichwald from Latvia (Ivanov et al. 1996), and the Late Devonian *Remigolepis* from Australia (Johanson 1997). Morphotypes of scales and zones of squamation described for *Asterolepis ornata* based on the studies of both juvenile and adult specimens from the Lode clay pit could be used for the comparison and description of isolated scales.

Recently exclusively well-preserved specimen of *Byssacanthus dilatatus* (Eichwald) with almost complete squamous part of the body has been found in the deposits of the Narva Regional Stage (Eifelian, Middle Devonian) in the outcrop along the Lemovzha River (Leningrad Region, Russia). Scales are rhomboid with rounded anterior margin. Ornamentation consists of a network of tiny sinuous ridges and elongated tubercles. Short elevated median crest is situated in the anterior portion of the scale. Scales from the anterior part of the squamation are more isometric and become longitudinally elongated with pointed anterior margin close to the caudal fin.

Two specimens of *Asterolepis* cf. *dellei* Gross (one complete skeleton and one partial squamation of the tail) from the Givetian Gremyaschiy Formation of October Revolution Island (Severnaya Zemlya Archipelago, Russia), demonstrate scales from all five zones of the scale morphotypes described for *A. ornata* (Ivanov et al. 1996). Flank scales of *A.* cf. *dellei* show overall similarity to, but are smaller than those of *A. ornata*; however, fulcral scales are much higher and elongated with narrower overlapping areas. Recently one specimen of *Asterolepis radiata* Rohon of small size with the complete armour and disarticulated scales behind the armour has been collected in the lowermost Frasnian deposits (Upper Devonian) cropping out along the coast of the Onega Lake at Andoma Hill (Vologda Region, Russia). Scales of *A. radiata* are rather similar to those of *A. ornata*, but differ in the more pronounced

ornamentation of ridges and tubercles on the scales probably belonging to the morphotype from the zone A, and more smooth scales of possibly of morphotype from the zone B (below the dorsal fin).

Most probably, the squamation in asterolepid antiarchs was developed ontogenetically in the similar cycle as the armour, but with retention, especially in the caudal part. The scales of morphotype of the zone A possess all three layers of the bone tissue, but the scales of morphotype of the zone D have the upper compact layer. Possibly, the derma of asterolepids in the caudal region was thinner without the fibrous and papillary strata hence scale was formed without the tuberculated layer.

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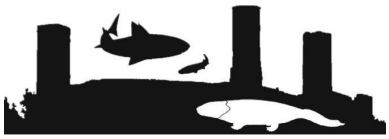
Johanson, Z. 1997. New *Remigolepis* (Placodermi; Antiarchi), from Canowindra, NSW, Australia. – *Geological Magazine*, **133**: 813-846.



Striatolamia tchelkarnurensa Glikman, 1964 – the final stage in the history of the shark genus in the Eocene

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The Palaeogene genus *Striatolamia* was established by Glikman (1964) based on the type species *Odontaspis macrota* Agassiz, 1843 in the family Odontaspididae Muler et Henle 1839. In that book he described (p.124) a new species, *S. tchelkarnurensis* (or more correctly *tchelkarnurensa,* according to the rules of the I.C.Z.N. (International Code…, 2000)), from the Late Eocene of the southern part of the Turgay Depression (Chegan Formation). The holotype is deposited in the Darwin Museum, Moscow. It contains an almost complete vertebrae column, scale fragments and about 30 teeth from one individual. The present study of the holotype shows clear distinctiveness of this species from other representatives of the genus. But the species still was not deservedly recognized probably because of lack of clear description and poor illustrations.

In 1999, Victor Zhelezko described the species *S. sibirica* with the similar dental morphology from the Chegan Formation of the north of the Turgay Depression (Zhelezko & Kozlov, 1999). This name should be recognized as a junior synonym, and *S. tchelkarnurensis* should be accepted as a valid species according to the Principle of priority of the I.C.Z.N. (International Code…, 2000).

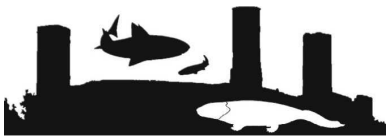
Striatolamia tchelkarnurensa is a final, Barton-Priabonian stage of the genus history. It differs from other species of *Striatolamia* by larger teeth, stronger crowns of the anterior teeth, greater mesiodistal width and labio-lingual flattening of the crowns on the lateral teeth,

and by the triangular shape of cusplets on the most of lower lateral and many upper lateral teeth. The enameloid on the lingual side of the crown is covered by very thin, slightly prominent striation.

Glikman, L.S. 1964. Sharks of the Palaeogene and their stratigraphic significance. M-L.: 229 p. [in Russian]

International Code of Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature. Transl. from Engl. and Fr. – Spb., 2000: 221 p. [in Russian]

Zhelezko, V.I. & Kozlov, V.A. 1999. Elacmobranches and Biostratigraphy of the Palaeogene of the Trans-Urals and Middle Asia. Materialy po stratigraphii i palaeontologii Urala. 3. Ekaterinburg: UrO RAN. 324 p. [in Russian]



Silurian cyathaspidid heterostracans of the Baltica and Kara terranes

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In the Silurian, cyathaspidid heterostracans were geographically widely distributed, and also spread to the Baltica and Kara continents. Their perfectly preserved head shields and/or macroscopic shield remains from this area have been described by J. Kiaer (1932: Gotland Island), D. Obruchev (1938: Belaya River basin, Southern Urals), L. Novitskaya (1970: Vaigach Island, north from Polar Ural), T. Märss (1977a, b: East Baltic) and M. Dek (2015: Poland), while Kunth (1872) and Geinitz (1884) found cyathaspidids from the erratic boulders in Germany and Poland.

The new reviewed material was obtained in the period from 1970 to 1990 from the drill cores of Saaremaa Island, East Baltic and Timan-Pechora Region as well as from the outcrops along the riverbank of the Tabuska River, Central Urals and on the October Revolution and Pioneer islands, Severnaya Zemlya. Specimens found by A. Blohin and D. Obruchev from the Belaya River basin, and shortly described by Obruchev (1938), will be re-described.

New specimens of the following genera were found: *Archegonaspis* Jaekel, *Tolypelepis* Pander and *Cyathaspis*? Lankester (as in Obruchev, 1938). A new *Archegonaspis* and one (or two?) new *Tolypelepis* species were identified. The new material indicates more variety in plate sculptures than previously known, and details the plate morphology. The material complements the taxonomical content as well as the spatio-temporal distribution of the family *Cyathaspididae*.

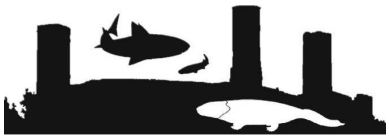
Dec, M. 2015. A new tolypelepidid (Agnatha, Heterostraci) from the Late Silurian of Poland. — *Journal of Paleontology*, **89**: 637–644.

Märss T. 1977a. Structure of *Tolypelepis* from the Baltic Upper Silurian. — *ENSV TA Toimetised. Keemia. Geoloogia*, **26**: 57-69.

Märss T. 1977b. The Upper Silurian cyathaspid *Archegonaspis* from the East Baltic. — *ENSV TA Toimetised. Keemia. Geoloogia*, **26**: 129-133.

Novitskaya, L. I. 1970. Late Silurian *Archegonaspis* from the Island Vaigach. — *Palaeontological Journal*, **3**:105-113. (In Russian).

Obruchev, D. 1938. Upper Silurian and Devonian Vertebrates of the Urals. — *Materials of the Central Scientific Geological Research Institute* [ЦНИГРИ], **2**: 36-43. (In Russian).



Gill rakers and teeth of three pleuronectiform species (Teleostei) of the Baltic Sea: a microichthyological approach

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In this microichthyological study (Märss et al., 2017) we SEM imaged, described and compared the mineralized substance of the gill raker cores of three pleuronectiform species, as well as the teeth of the jaws and the branchial tooth plates, and we compare them to the teeth on the rakers. Such work was carried out for the first time. Studied species were the European plaice *Pleuronectes platessa* Linnaeus and European flounder *Platichthys flesus trachurus* (Duncer), both in the Pleuronectidae, and turbot *Scophthalmus maximus* (Linnaeus) in the Scophthalmidae. The mineralized substance of the raker cores gives them their shape. We follow how the rakers differ from the 1st to 4th gill arches and how some features change during ontogeny. This microichthyological study can serve as a model for similar studies of Palaeozoic fishes, providing informative comparisons with microscopic bony structures such as those in the buccopharyngeal region of early vertebrates.

Answering the question (Märss et al., 2017, p. 44), 'Can gill rakers and teeth of pleuronectiforms be useful in taxonomy and phylogeny?' we found that specimens revealed features that separate the plaice from the flounder, and distinctively characterize the turbot, which has ossicles completely different from the others. Detailed features of the rakers and teeth also vary ontogenetically as well as among branchial arches within species. The morphology of the rakers as well as that of the teeth on jaws and branchial tooth plates have taxon-specific characters (studied by us at the generic level). Reliable characteristics are the shapes of raker cores, the pattern of fine structures on raker cores and the size, shape and placement of teeth in jaws and tooth plates. Among the three studied pleuronectiforms only turbot has true teeth on its rakers (still, their histology needing more studies). This microichthyological research along with our earlier investigations (Märss et al., 2015) allows the identification of pleuronectiforms from their dermal tubercles, the morphology and arrangement of teeth on jaws and on tooth plates in the pharynx, the gill rakers covered with soft tissue, with or without teeth, and the bony cores of gill rakers. When similar detailed SEM studies are completed in related taxa, these features can be utilized not only in taxonomy but also in phylogeny, palaeontology and zooarchaeology. We further concluded that the teeth found on branchial toothplates in all three studied species and in the turbot on the gill rakers are true teeth (Sire & Huysseune, 2003) with acrodine caps and Type 2 tooth attachment (Fink, 1981). Our examination of such structures in the Pleuronectiformes suggests that they are useful in flatfishes not only as dietary indicators but also as taxonomic and phylogenetic characters, unlike the example discussed by Liston (2013).

Fink, W. L. 1981. Ontogeny and phylogeny of tooth attachment modes in actinopterygian fishes. – *Journal of Morphology*, **169**: 167–184.

Liston, J. 2013. The plasticity of gill raker characteristics in suspension feeders: implications for Pachycormiformes. *In*: Arratia, G., Schultze, H.-P. & Wilson, M. V. H. (eds), *Mesozoic Fishes 5. Global Diversity and Evolution*, pp. 121–143. Verlag Dr. Friedrich Pfeil, München, Germany.

Märss, T., Wilson, M. V. H., Lees, J., Saat, T. & Špilev, H. 2015. A comparative SEM study of ossicles in the Pleuronectiformes (Teleostei) of the Baltic Sea – *Proceedings of the Estonian Academy of Sciences*, **64**: 495–517.

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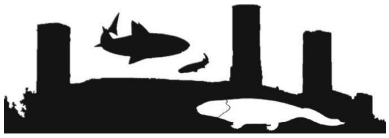

On the vascularization in earliest shark teeth; an approach from computed tomography

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Histologically the teeth of elasmobranchs are formed by two highly mineralized tissues, the dentine and the enameloid. Depending on the presence and location of the two conformations of dentin, osteodentine and orthodentine, and the presence or absence of pulp cavity, the teeth of have traditionally been classified into two different histotypes, osteodonts or orthodonts (Thomasset's 1930; see also Moller et al. 2015 and references). Some authors have considered that the orthodont histotype, -where the pulp cavity remains present in adult teeth, orthodentine form the crown under the enamaloid layer and trabecular dentine being only at the base- is the plesiomorphic condition for chondrichthyans (e.g. Zangerl, 1981).This classification however is a simplified approach as some exception to this "clasical" histotypes can be found among neoselachians (e.g. Moller et al 2015). This seems more evident were fossil taxa are considered.

Leonodus carlsi and *Celtiberina Maderi* are the oldest known tooth-bearing shark up to date (Botella et al., 2009). The primitive morphologic and histologic features of these teeth locate this taxon in a relevant position in the phylogeny of chondrichthyans .

Here we present for the first time a digital reconstruction in 3D of the vascular pattern and microstructure of *Leonodus* and *Celtiberina* teeth. The specimens were extracted from limestone samples from several levels in the Lockhovian (Lower Devonian) of the Nogueras Fm. (Celtiberia, Spain) (see Carls, 1988), using formic acid (5-10%). Afterwards, they were scanned using Synchrotron X-Ray Tomographic Microscopy (SXRTM) at the TOMCAT beamline (Swiss Light Source) from the Paul Scherrer Institute. Tomographic reconstructions were visualised and analysed using Avizo, were the vascular system was virtually extracted.

The material is deposited in the Museum of Paleontology at the University of Zaragoza (MPZ) and at the Museum of Geology of the University of Valencia (MGUV).

The vascular systems of teeth in both taxa are similar, showing a complex network of vascular channels ("horizontal" and "ascending") that run through the entire tooth, together with a large principal chanal, crossing the tooth linguo-labially, which can or not bifurcate. This vascularization pattern is compared, in a phylogenetical context, with available dates from other basal chondrichthyans and " acanthodian tooth whorls".

This work has been founded by the Spanish Research Project CGL2014-52662-P and by the Generalitat Valenciana Research Project GV/2016/102.

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Carls, P. 1988. The Devonian of Celtiberia (Spain) and Devonian Paleogeography of SW Europe. – *In McMillan, N.J., Embry, A.F. & Glass, D.J. (Eds.). Devonian of the World (Proceedings of 2nd International Symposium on the Devonian System, Calgary, 1987. Canadian Society of Petroleum Geologist, Calgary.*

Moyer, K.M., Riccio, M.L. & Bemis, W.E. 2015. Development and Microstructure of Teeth Histotypes in the Blue Shark, *Prionace glauca* (Carcharhiniformes: Carcharhinidae) and the Great White Shark, Carcharodon carcharias (Lamniformes: Lamnidae). – *Journal of Morphology*. **276**: 797-817.

Thomasset, J.J. 1930. Recherches sur les tissus dentaires des poissons fossiles. – *Arch. Anat. Histol. Embryol,* **10**:5–153.

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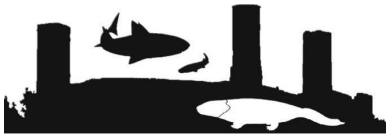

Using computational fluid dynamics to study the hydrodynamic performance of extinct jawless vertebrates

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[2] School of Earth Sciences, University of Bristol, Bristol, UK; *Phil.Donoghue@bristol.ac.uk*
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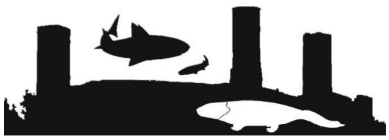
Most of the Palaeozoic agnathans were armoured forms (e.g. heterostracans, osteostracans, galeaspids and pituriaspids), characterised by having a large, rigid external shield enclosing the anterior part of the body. This, together with the lack of pectoral fins have traditionally interpreted as indicative of poor swimmers, mainly bottomliving forms with little manoeuvrability. However, the functional significance of their rigid carapaces remains

unclear, and in fact, the great disparity of morphologies present among the cephalic shields of armoured jawless, the development of fixed exoskeletal elements with clear hydrodynamic importance, (i.e. lateral expansions, dorsal spines or keels, large rostrums), suggest that agnarthan carapaces were clearly related with hidrodinamic funtions (Botella & Fariña, 2008) Interestingly, Galeaspids and Osteostracans show a similar range of forms acquired independently in each linage in different geographical regions. Thus, the study of such taxa provides a great opportunity to analyze whether this morphological convergence was the result of equivalent functional adaptations to similar aquatic environment. Given this scenario, we have analysis the shape variation of 70 species of galeaspids and osteostracans using geometric morphometrics and tested the hydrodynamic performance of the most extreme forms using computational fluid dynamics simulations.

Our results show that both groups occupy broadly the same areas of the morphospace, explaining the three first Principal Components the 95% of the total shape variance. In addition, comparison of the hydrodynamic performance (based on drag and lift forces and their coefficients) of a selection of taxa representing the extremes of the morphological variation, allowed us to better understand variations in morphology (development of the snout, cornual processes, fusiform bodies, etc.) in terms of swimming strategies and modes of life. This methodology opens up a new opportunity to investigate the ecology of these groups of early vertebrates.

This work has been founded by the Spanish Research Project CGL2014-52662-P and by the Generalitat Valenciana Research Project GV/2016/102.

Botella, H., & Fariña, R. A. 2008. Flow pattern around the rigid cephalic shield of the Devonian agnathan Errivaspis waynensis (Pteraspidiformes: Heterostraci). – *Palaeontology*, **51:,** 1141-1150.



The earliest tetrapod tracks from Zachełmie Quarry, Holy Cross Mountains, Poland

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Ten tetrapod trackways and numerous isolated tracks (manus and pes imprints) have been discovered in the Middle Devonian Wojciechowice Formation of the Holy Cross Mountains, Poland (Niedźwiedzki et al., 2010; in prep.). These trackways display a wide variety of behavioural, gait and substrate related extramorphologies. They clearly document semi-terrestrial or underwater walking, resting and swimming phases of locomotion. The traces occur at three horizons (A-C) within cyclic deposits with clayey-dolomitic shales and dolomite mudstones (Narkiewicz et al., 2015) characterized by: low-energy deposition; abundant evaporation with repeated desiccation events; palaeosol developments; microbial colonization; fossils of charophytes and early vascular plants; a monospecific ostracod assemblage; large arthropod burrows; and a *Cruziana* ichnofacies with a lack of marine

invertebrate taxa (Qvarnström et al., in prep.). Morphological and ichnological analyses of the trackways and tracks suggest they were made by tetrapods ranging in body length approximately from 0.4 to 2.3 m (scale based on *Ichthyostega*), which moved in some cases as a typical quadrupedal animal (traces arranged in diagonal stride sequence), but more often produced a ladder-like and narrow set of imprints, sometimes with alternating shallow and deep impressions. This suggests two very different modes of locomotion. Integrating ichnological and facies data from the Zachełmie section with anatomical information from known Late Devonian tetrapods, we suggest that the earliest tetrapod locomotion was performed in two ways: 1) in shallow water, or underwater, with a rigid sprawling posture with the trunk lifted from the substrate, and limbs moving in an alternating "lateral sequence walk" pattern; 2) in shallow water or semi-terrestrial conditions, with limbs pointing to the bottom and locomotion based on repulsion action, with left and right limbs moving together. Analysis of well-preserved skeletal fossils from the Late Devonian of Greenland suggests that early tetrapods were adapted for both lateral (*Acanthostega*) and dorsoventral (*Ichthyostega*) flexion of the axial skeleton (Ahlberg et al., 2005). It is uncertain whether the trackway diversity at Zachełmie reflects locomotory flexibility in one taxon or the presence of several taxa. Some isolated tracks from Zachełmie show large proximal or lateral displacement rims, and short triangular or long curved digit impressions. Comparison of the best preserved specimens with known early tetrapod limb skeletons indicates that the prints include the ventral surface of the lower leg and knee. Preliminary three-dimensional models of the Middle Devonian tetrapod hand and foot morphology based on extensive examination of well-preserved ichnological material are proposed (Niedźwiedzki et al., in prep). The sedimentological and facies analysis of the trackway-bearing sequences from Zachełmie suggests a shallow-water non-marine environment with repeated subaerial exposure and clearly implies that tetrapods had already acquired terrestrial competence in the Middle Devonian.

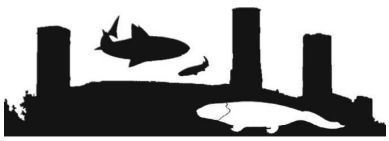
Ahlberg, P.E. et al. 2005. The axial skeleton of the Devonian tetrapod *Ichthyostega*. – *Nature* **437**: 137–140.

Narkiewicz, M. et al. 2015. Palaeoenvironments of the Eifelian dolomites with earliest tetrapod trackways (Holy Cross Mountains, Poland). – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **420**: 173–192.

Niedźwiedzki, N. et al. 2010. Tetrapod trackways from the early Middle Devonian period of Poland. – *Nature* **463**: 43–48.

Niedźwiedzki, N. et al. (in prep). Early tetrapod trace fossils from the Middle Devonian of the Holy Cross Mountains, Poland.

Qvarnström, M. et al. (in prep.). Non-marine palaeoenvironment associated to the earliest tetrapod tracks.



The Middle Devonian tetrapod trackways from Valentia Island, Ireland – new observations and discoveries

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Numerous tetrapod trackways have been described from the Middle Devonian (late Givetian) continental Valentia Slate Formation of Valentia Island, Ireland (Stössel, 1995, 2000; Stössel et al., 2016). New trackways and tracksites were discovered in September 2016 on the north-eastern coast of Valentia Island in County Kerry. The revision of previous finds and the analysis of the new material provide data towards an understanding of the limb anatomy and mode of locomotion of the late Middle Devonian tetrapods. Most trackways are partly eroded or tectonically deformed, but are preserved well enough to be assigned to ichnorecord of the early tetrapods with: 1) four limbs; 2) limbs bearing five or more, rather short and broad, clawless digits; 3) manus surface clearly smaller than pes. Trackways do not show any clear sign of body or tail drag marks. A central groove and undulating furrow seen at the beginning of one trackway, interpreted as tail and body drag marks (see Stössel et al., 2016), may represent a resting trace. Additional analyses of the trackways suggest they were made by populations of similar tetrapods, but of slightly varying in size (estimated total body length between 0.4-1.2 m). The Valentia Island tetrapods inhabited marginal environments of proximal river channels (Stössel et al., 2016) and are only slightly younger (4-5 million years) than the earliest tetrapod ichnorecord from Poland (Niedźwiedzki et al., 2010; Narkiewicz et al., 2015). Furthermore, excellent outcrops and abundance of trackway preservation and also presence of body fossils in the Valentia Slate Formation offer potential for the clarification of the evolutionary history of Middle Devonian tetrapods.

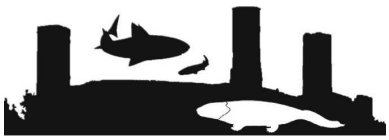
Narkiewicz, M. et al. 2015. Palaeoenvironments of the Eifelian dolomites with earliest tetrapod trackways (Holy Cross Mountains, Poland). – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **420**: 173–192.

Niedźwiedzki, N. et al. 2010. Tetrapod trackways from the early Middle Devonian period of Poland. – *Nature* **463**: 43–48.

Stössel, I., 1995. The discovery of a new Devonian tetrapod trackway in SW Ireland. – *J. Geol. Soc. Lond.* **152**: 407–413.

Stössel, I., 2000. Frühe Tetrapoden: Kontroverse Spurenfossilien. – *Neujahrsbl. Zür. Naturforsch. Ges*. **145**: 31–40.

Stössel, I., Williams, E.A., Higgs, K.T. 2016. Ichnology and depositional environment of the Middle Devonian Valentia Island tetrapod trackways, south-west Ireland. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **462**: 16–40.



New data on the microstructure of acanthodian scale enameloid.

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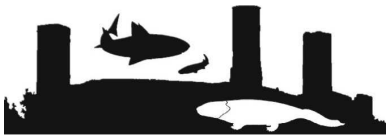
Microstructure of enameloid of five scales, defined as Acanthodiformes? indet and *Cheiracanthus* aff. *C. latus* from the Eifelian and Givetian deposits (Narova, Aruküla and Burtnieki Regional Stages) of Leningrad Region, Russia has been studied. All the scales possess an ultrasculpture on the crown, consisting of microtubercles with a diameter of 1–5

μm (in C. aff. C. latus scales) and 1–2 μm (in Acanthodiformes? indet). In *C.* aff. *C. latus* scales (with ridged crown surface) the microtubercles tend to line up, forming thin longitudinal rows. Two types of ultrasculpture can be distinguished on the scales of Acanthodiformes? indet. In the first one the microtubercles tend to coalesce into the larger, second-order microtubercles with a diameter of 7–8 μm. In the second type they group into wavy longitudinal stripes 8 μm in width.

A clear hypermineralized tissue, forming upper portions of the crowns' growth lamellae is seen in thin sections of all the scales. It is birefringent in polarized light and shows rodlet arrangement. In etched (with 10% HCl) thin sections of enameloid of the Acanthodiformes? indet scale (with the ultrasculpture of the second type) closely packed, short crystallites, oriented subperpendicular to the surfaces of the growth lamellae are seen. This microstructure is reminiscent of that of *Palaeoniscum* sp. ganoin, described by Richter and Smith (1995). The major differences are that the crystallites are 1,5–2 times smaller and no incremental lines can be seen. Individual crystallites couldn't be distinguished in other scales, although they possess incremental lines within each growth lamella. The microstructure of their enameloid is close to that of "sponge-like" ganoin of *Cheirolepis trailli*, described by the same authors. The microstructure of enameloid of the studied acanthodian scales seem to be close to that of ganoin of Actinopterygii.

Richter M. & Smith M. 1995. A microstructural study of the ganoin tissue of selected lower vertebrates. – *Zoological Journal of the Linnean Society*, **114**: 173–212.



The evolution of tooth replacement and tooth resorption in Osteichthyes

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[3] Curtin University, Bentley, Australia; *k.trinajstic@curtin.edu.au*
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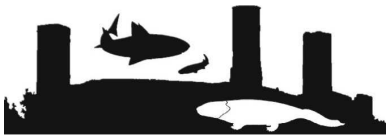
Tooth replacement is a character of extant gnathostomes with tooth families resembling a conveyor belt in Chondrichthyes and intraosseus tooth replacement in Tetrapoda including humans. In Osteichthyes tooth replacement is linked with resorption before shedding, whereas in Chondrichthyes teeth are shed without resorption. Basal conditions and the origin of tooth replacement and resorption in Osteichthyes are debated (Cunningham et al. 2012, Chen et al. 2016). Comparative data on tooth replacement and resorption of fossil and recent taxa are rare.

We use digital, non-destructive methods including Micro-CT and Synchrotron microscopy (SRXTM) to identify lines of arrested growth and resorption lines as evidence to reconstruct sclerochronology. Detailed 3D segmentation in submicron scale of articulated undebated jaws and teeth of recent and fossil osteichthyans allows an identification of replacement mechanisms in teeth and oral denticle morphotypes.

Resorption lines in *Polypterus* and *Moythomasia* are continuous proximal to the replacement teeth and can erode deeply, erasing parts of initial teeth completely or only partially. Oral denticles e.g. in *Moythomasia* are not replaced, but added appositionally. Although dental morphologies in *Moythomasia* are different their replacement and resorption are similar in contrast to oral denticles that differ in morphology and replacement. These first results will facilitate an interpretation of mechanisms in fragmentary material and evolution of tooth resorption in Osteichthyes.

Chen, D., Blom, H., Sanchez, S., Tafforeau, P. & Ahlberg, P.E. 2016. The stem osteichthyan *Andreolepis* and the origin of tooth replacement. Nature **539**: 237–241.

Cunningham, J. A., Rücklin, M., Blom, H., Botella, H. & Donoghue, P. C. J. 2012. Testing models of dental development in the earliest bony vertebrates, *Andreolepis* and *Lophosteus*. – *Biology Letters* **8**: 833–837.



Paleozoic jawless fishes exhibited body form-dependent modes of habitat use and dispersal.

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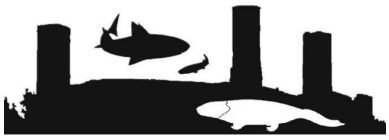
Habitat shifts are a critical driver of speciation and novelty in fishes; populations in distinct environments frequently exhibit divergent forms. Despite the wide variety of body forms observed in Paleozoic fishes – jawed and jawless – we know little about their environmental context or the relationship with dispersal during the initial diversification of vertebrates. In order to track the habitat distribution of mid-Paleozoic fishes, we assembled benthic assemblage zone data for the fossil records of major agnathan lineages. We used Bayesian methods of discrete ancestral state reconstruction to determine changing habitat preferences through time, and coded for functionally significant body traits to determine environmental associations. We find that, at the broadest scale, all major vertebrate clades originated in a restricted set of habitats at the shallow margins of ancient seas. However, various Silurian-Devonian jawless fishes later dispersed into a range of zones from freshwater to reef to open ocean. Distinct body forms were associated with these habitats and dispersal activity, a pattern consistent with modern teleost groups, such as sticklebacks and reef fishes. However, shifts into offshore environments by the most widely dispersed groups (e.g. thelodonts, crown gnathostomes) do not appear to have coincided with renewed high-level diversification. Our results suggest generally nearshore origins for vertebrates, underpinning an onshore-offshore trend like that of benthic invertebrates. Changing breadth and availability of nearshore habitats, perhaps driven by global environmental changes, likely played a role in early

vertebrate diversification, while novel forms enabled greater dispersal, establishing modern modes of habitat use.



Early ray-finned fishes from the Late Devonian Catskill Delta of Pennsylvania, USA

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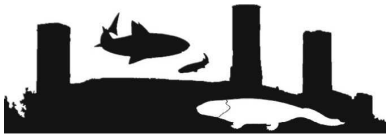
A sparse fossil record plagues the early history of the 'ray-finned' fishes (Actinopterygii). This rarity is taken to reflect a lack of abundance of actinopterygians in Devonian ecosystems, and imply they occupied minor ecological roles. New actinopterygian fossils collected from the Late Devonian (Famennian Stage) Catskill Formation of Pennsylvania may help clarify the relationship between local morphological disparity and habitat partitioning among freshwater, ray-finned fishes. A nearly complete fish and a partial second specimen, preserved on part-counterpart slabs, represent a new taxon. These fish belong to the rich vertebrate assemblage found at the Red Hill road cut locality, which includes an acanthodian, placoderms, chondrichthyans, sarcopterygians (including several tetrapods), and a single, previously described actinopterygian, *Limnomis delaneyi* Daeschler (2000). Specimens of the new fish taxon preserve much of the skull, fins, and squamation. Taxonomically relevant characters include the presence of dermohyals, pectoral fins with fringing fulcra, and pelvic fins. In addition, preliminary micro-CT scans of the most complete specimen show that gill arches are preserved within the matrix. The new taxon and *Limnomis* are found in different taphofacies at Red Hill, which suggests the existence of habitat partitioning among ray-finned fishes in the Catskill Delta Complex. A large fish specimen discovered at another Catskill road-cut exposure indicates the presence of a third actinopterygian. However, the poor condition of the skull precludes a precise knowledge of its affinities. Continued sampling of well-studied fossil localities in Pennsylvania has improved the early fossil record of the Actinopterygii. If early ray-finned fishes prove to be more ecologically diverse than was previously understood, then new discoveries may force a revision of ecological hypotheses for the subsequent diversification of these fishes.

Daeschler, E.B. 2000. An early actinopterygian fish from the Catskill Formation (Late Devonian, Famennian) in Pennsylvania, U.S.A. – *Proceedings of the Academy of Natural Sciences of Philadelphia*, **150**: 181-192.



New data on *Sagenodus* from the Upper Carboniferous-Lower Permian of the Czech Republic

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[3] Institute of Geology of the CAS, v. v. i., Rozvojová 269, CZ-165 00 Praha 6, Czech Republic; *zajic@gli.cas.cz*

Antonín Frič (Anton Fritsch) described an extensive material of *Sagenodus* from the Upper Carboniferous-Lower Permian deposits of Czech Republic in 1888. The most numerous and best preserved fossils come from the Upper Carboniferous (Stephanian C) Kounov locality (Kladno Basin). This material consists of isolated skull bones (with an exception of three specimens having few bones in articulation), elements of postcranial skeleton, tooth plates in different growth stages, few scales and one semi-articulated individual. Frič (1874) raised a new specific name for this material – *Ceratodus barrandei*, but in 1888 he placed it in *Ctenodus obliquus* Hancock & Atthey, 1871. The latter species was assigned to *Sagenodus inaequalis* Owen, 1867 by Woodward in 1891. Here we present a preliminary reconstruction of the skull roofing bones of this dipnoan which is compared with skull roofs of other *Sagenodus* members known today from Germany, Great Britain and USA. The skull as well as tooth plates of *Sagenodus* from Kounov are similar to those of other representatives of this genus. Frič (1888) described also few *Sagenodus* scales from the Upper Carboniferous (Westphalian D) Nýřany locality (Plzen Basin). Another material comes from the Lower Permian Košťálov locality (Krkonoše Piedmont Basin) and consists of a complete individual with poorly preserved skull region. It was assigned to *Sagenodus tardus* (Frič, 1888), but state of preservation of this specimen does not allow to make any specific identification. Some new *Sagenodus* fossils (mostly scale fragments) have been discovered in old Frič's localities and in few new sites in Czech Republic in the last decades (e.g., Zajíc & Štamberg 1985, Štamberg & Zajíc 2008). All these findings show that *Sagenodus* was a common member of the Upper Carboniferous-Lower Permian ichthyofauna of the Bohemian region.

Frič, A. 1874. Uber die Entdeckung eines Lurchfisches: *Ceratodus Barrandei* in der Gaskohle des Rakonitzer Beckens. – *Sitzungsberichte der königl. böhm. Gesellschaft der Wissenschaften in Prag*, **7**: 193-195.

Fritsch, A. (Frič, A.) 1888. Die Lurchfische, Dipnoi. Nebst Bemerkungen über silurische und devonische Lurchfische. – *In*: *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens*, **2** (3), pp. 65-92. *Selbstverlag*, Prag.

Hancock, A. & Atthey, T. 1871. A few remarks on *Dipterus* and *Ctenodus* and their relationship to *Ceratodus forsteri*, Kreft. from the Natural History. – *Transactions of Northumberland and Durham*, **7**: 190-198.

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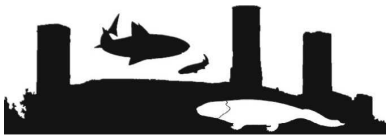

Hagenoselache and the postcranial skeleton of the early xenacanth sharks

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Early xenacanths are mainly known by isolated dermal remains (teeth, spines and scales) (Turner & Burrow, 2011 and references therein) and only two species, *Diplodoselache woodi* (early Viséan; Midland Valley, Scotland) and *Hagenoselache sippeli* (Namurian B; NW Sauerland, Germany), are described on articulated skeletons (Dick, 1981; Hampe & Heidtke, 1997). *Hagenoselache*, originally defined for a fragmentary skeleton of a single individual, is a key-taxon stratigraphically located between the Viséan stem-xenacanth *Diplodoselache* and the post-Namurian crown-xenacanths (e.g., *Lebachacanthus*, *Orthacanthus*, *Xenacanthus* and *Triodus*), many of them known by articulated complete skeletons (Soler-Gijón, 2004).

Here we report a second specimen of *Hagenoselache sippeli*, coming from the type locality. The new material representing a near-complete and partially disarticulated skeleton, improves the diagnostic definition of the genus and provides valuable data for future phylogenetic analyses of xenacanths and other Paleozoic chondrichthyans. The new specimen confirms the presence of a dorsal dermal spine in front of the elongated dorsal fin in *Hagenoselache* as other xenacanths. The spine, not visible in the holotype, is slender and appears close to the occipital region of the neurocranium suggesting a cervical position in life similar to the derived xenacanths. The pectoral fin is axial, biserial, with at least 13 large preaxial radials and 4 postaxial radials in a distal position. The second anal fin, (previously identified as the inferior lobe of a heterocercal caudal fin) is well preserved in both specimens, and shows the posterior axis, typical for crown-xenacanths, with a few branching elements, similar to the condition in the anals of derived genera *Xenacanthus* and *Triodus*. The caudal fin (previously described as superior lobe of a heterocercal caudal fin) is similar to that in the primitive *Lebachacanthus*, showing an anterior part with a short but tall epichordal lobe with large radials and a posterior part at the very end of the tail composed by numerous vertebrae with small neural and hemal spines. In conclusion, *Hagenoselache* exhibits a mosaic of xenacanth characters with the mix of derived dorsal and anal fins and a primitive caudal fin which anatomically differs from the true heterocercal caudal fin of the stem *Diplodoselache*.

Dick, J.R.F. 1981. *Diplodoselache woodi* gen. et sp. nov., an early Carboniferous shark from the Midland Valley of Scotland.– *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **72**: 99-113.

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Soler-Gijón, R. 2004. Development and growth in xenacanth sharks: new data from Upper Carboniferous of Bohemia.– *In*: G. Arratia, M.V.H. Wilson & R. Cloutier (Eds.), *Recent Advances in the Origin and Early Radiation of Vertebrates*, pp. 533-562. *Verlag Dr. Friedrich Pfeil*, München.

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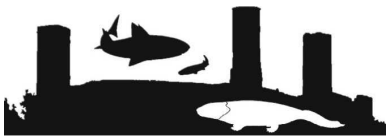

Ecomorphology of *Tanyrhinichthys mcallisteri*, a long rostrumed actinopterygian fish from the Kinney Brick Quarry, New Mexico

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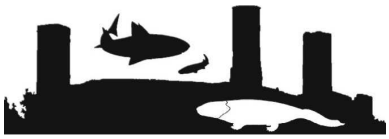
The Upper Pennsylvanian (Missourian) sediments of the Kinney Brick Quarry (KBQ) in New Mexico contain a diverse and well preserved fish assemblage from the Atrasado Formation. Actinopterygians and acanthodians are commonly collected from KBQ, with sharks and coelacanth rare but diverse within this assemblage. A unique fish known only from KBQ, *Tanyrhinichthys mcallisteri* is a small actinopterygian with an lengthened rostrum and elongated body. Previously, *T. mcallisteri* was known only from a single partially complete specimen. New work has recently revealed six new complete and partial specimens of this fish, enabling a more detailed morphological and ecological analysis which is presented here. The new specimens demonstrate variation in body size and rostrum length. This suggests that *Tanyrhinichthys* may have exhibited sexual dimorphism with males having longer rostrums and more gracile bodies and with females having proportionately shorter rostrums and more robust bodies. Previous descriptions suggested that *Tanyrhinichthys* was an ambush predator similar to the modern pike (*Esox*) and gar (*Lepisosteus*) based on its slender body and elongate rostrum. However, the new material indicates that it was a bottom feeder morphologically similar to the modern sturgeon (*Acipenser*). Like sturgeon, *T. mcallisteri* had a long anal fin set farther forward than the dorsal, a small, shallowly cleft caudal fin, an elongate, pointed rostrum, a small, subterminal mouth, small teeth, large lateral line scales, and an anteriorly deepened and caudally tapering body that would have allowed it to feed and swim in a manner similar to sturgeon. Two other long-rostrumed actinopterygians, an unnamed taxon from Indiana and *Phanerorhynchus* from the U.K., are known from the similarly-aged, Pennsylvanian coal deposits. *Phanerorhynchus* is similar to *Tanyrhinichthys* in fin morphology, mouth placement and size, and overall morphology, differing largely in its

spine-like fin rays. The unnamed taxon from Indiana is known only from a skull bearing an elongate rostrum, which is similar in size and shape to the specimens of *Tanyrhinichthys* that exhibit sexually dimorphic male traits. Further analysis will show whether these represent a short-lived, freshwater Euramerican clade or convergent but widespread morphotype among Paleozoic fishes.



Presumptive coelacanth remains from the Middle Triassic of Poland

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In the European Early Triassic, the coelacanths are known only from the Upper Olenekian of Romania (Cavin & Grădinaru, 2014). The Middle Triassic coelacanths so far have been described from fairly complete skeletons from the Middle-Late Anisian of Luoping Biota of southwest China (Wen, 2012).

Herein we report the first occurrence of Coelacanthiformes in the Gogolin Formation of Upper Silesia (Poland) and the Lower Muschelkalk strata around Rüdersdorf (Germany).

One of the five dermal plates coming from several localities in Poland (Żyglin, Sosnowiec) was sectioned for histology, and they were interpreted as coelacanth dermal bone based on detailed microstructural and histological studies. They show an unusual appearance in the macroscopic view: all of the specimens are characterized by a regular sculpturing composed of roughly hexagonal fields, each with a medial protuberance bearing a single, conical denticle composed of orthodentin. The denticles are varied in size, hollow, and some of them are broken, exposing their pulp cavities. The specimens are convex externally and slightly asymmetrical, but all of them have roughly the same morphology and shape. Therefore, their morphology is not consistent with the occlusive pattern of ganoid fish dental batteries nor ornamented armor plates of sympatric cyamodontid placodonts (Rieppel, 2002) or any other tetrapod osteoderms. A similar dermal plate morphology was illustrated by Hermann von Meyer (1847-1851, Pl. 31, Fig. 21).

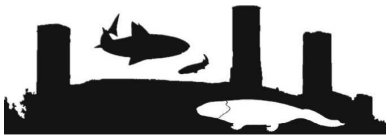
Our discovery shows that Coelacanthiformes are more commonly found in Lower Muschelkalk than it was previously thought.

Cavin, L., and Grădinaru, E. 2014. *Dobrogeria aegyssensis*, a new early Spathian (Early Triassic) coelacanth from North Dobrogea (Romania): *Acta Geologica Polonica*, **64**: 161-187.

Meyer H. von (1847-1855) Zur Fauna der Vorwelt. 2 Abt. Die Saurier des Muschelkalkes mit Rücksicht auf die Saurier aus Buntem Sandstein und Keuper, 167 pp + 70 plates. Frankfurt a. Main.

Rieppel, O., 2002. The dermal armor of the cyamodontoid placodonts (Reptilia, Sauropterygia): morphology and systematic value. *Fieldiana Geology*, **46:** 1-41.

Wen, W., 2012, Coelacanths from the Middle Triassic Luoping Biota, Yunnan, South China, with the earliest evidence of ovoviviparity. *Acta Palaeontologica Polonica*, **58**: 175-193.



First attested placoderms from the "placoderm sandstone" in the Lower Devonian (Emsian) of the Holy Cross Mountains, Poland

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The "Placoderm Sandstones" is a term introduced by Gürich (1896) for a mass-occurrence of vertebrate remains considered to be placoderms. Paradoxically, no placoderm from the "placoderm sandstone" has never been formally described for more than 120 years.

The Placoderm Sandstone exposed in the abandoned quarry at Podłazie Hill in the Holy Cross Mountains, Poland, was recently revisited and excavated during field work. Bone-bearing breccia was studied in details for the first time and subjected to taphonomic analysis (Szrek et al. 2014). Correlations and palynological analyses indicate a most likely upper Emsian age for the Podłazie Hill specimens considered herein. Vertebrate remains are dominated by heterostracans, while true placoderms compose less than 20% of the total vertebrate assemblage. The high degree of fragmentation of the bones and low degree of abrasion indicate that the remains were reworked and transported before final burial during a storm event.

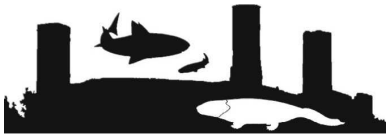
A detailed study of the vertebrate assemblage from the Placoderm Sandstone from Podłazie Hill in the Holy Cross Mountains reveals that some of the remains can be attributed to the genera *Kujdanowiaspis* and *Erikaspis,* among other unspecified actinolepids and brachythoracids (Szrek & Dupret, in prep.). The actinolepid material is characterised by bigger sizes than Podolian specimens in Ukraine which may be related to geographic variation. According to the proximity between Podolia and the Holy Cross Mountains it is likely that the Polish *Kujdanowiaspis* sp. may be a successor of some species from the Pragian of Podolia and/or the Lochkovian of Spain. Anterolateral plates provisionally assigned to Arthrodira indet. probably represent a new taxon due to the high overlapping surface for median dorsal and anteroventrolateral plates.

Dupret, V., Carls, P., Martínez-Pérez, C. & Botella, H. 2011. First Perigondwanan record of actinolepids (Vertebrata: Placodermi: Arthrodira) from the Lochkovian (Early Devonian) of Spain and its palaeobiogeographic significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **310**: 273–282.

Gürich, G. 1896. Das Paläozoicum im Polnische Mittelgebirge. *Verhandlungen der Russichen-Kaiserlichen Mineralogischen Gesellschaft zu St-Petersburg*, **2**: 1–539.

Szrek, P., Niedźwiedzki, G. & Dec, M., 2014. Storm origin of bone-bearing beds in the Lower Devonian placoderm sandstone from Podłazie Hill (Holy Cross Mountains, central Poland). *Geological Quarterly*, **58**: 795–806.

Szrek, P & Dupret, V. (in prep.). Placoderms from the "placoderm sandstone" in the Lower Devonian of the Holy Cross Mountains, Poland.



The Late Devonian eastmanosteid arthrodire from the Kowala Quarry, Holy Cross Mountains, Poland

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The various material from the Devonian of the Holy Cross Mountains assigned to the Dinichthyidae family have been described and/or mentioned in few papers (e.g. Kulczycki, 1957, Ivanov & Ginter, 1997, Szrek, 2008). Specimen from the Frasnian of Wietrznia Quarry described by Kulczycki (1957) as *Dinichthys pustulosus* and specimen from the uppermost Frasnian of Płucki regarded as the juvenile form of *Eastmanosteus*, have been assigned to the new species of the genus *Eastmanosteus* by Ivanov and Ginter (1997). This species, however, has never been formally described.

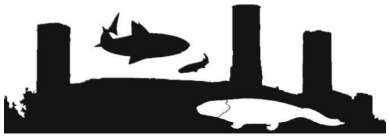
Newly collected material comes from the lower Famennian of the Kowala Quarry, in the western part of the Holy Cross Mountains. This is the head fragment of the right half of the skull-roof, 25 cm long. The posterior part of the specimen, which is comprising a part of paranuchal, marginal, part of central, preorbital and postorbital plates, demonstrates typical features for medium-size *Eastmanosteus pustulosus*. These features reflect those seen in the specimen described by Kulczycki (1957; *Dinichthys pustulosus*). However, relatively big orbits and elongated rostrum demonstrate unusual features of our species. Moreover, the age of this specimen is estimated on lower Famennian (Late *Palmatolepis marginifera – P. trachytera* Conodont Zone). Therefore it is the youngest occurrence of this genus, which traditionally has not been noted above the Frasnian-Famennian boundary.

Therefore, we agree with Ivanov and Ginter (1997) that the specimen described by Kulczycki (1957) as *Dinichthys pustulosus* represents a new species of *Eastmanosteus*, and our new specimen from Kowala belongs to this species. Morphology of the anterior part of the head visible on Kowala specimen will allow to supplement general description. We also postulate to regard that small skull from Płucki as a juvenile form of this new species (Ivanov & Ginter, 1997) rather than a separate species.

Ivanov, A. & Ginter, M. 1997. Comments on the Late Devonian placoderms from the Holy Cross Mountains (Poland). *Acta Palaeontologica Polonica*, **42**: 413 - 426.

Kulczycki, J. 1957. Upper Devonian fishes from the Holy Cross Mountains. *Acta Palaeontologica Polonica*, **2**: 285-380.

Szrek, P. 2008. Vertebrates from the upper Kellwasser limestone, Frasnian-Famennian boundary beds (Upper Devonian) of the Holy Cross Mountains (Poland). *68th Annual Meeting Society of Vertebrate Paleontology Cleveland, Ohio USA October 15-18, 2008, Journal of Vertebrate Paleontology*, **28**: 150.



A mechanism for tooth resorption in arthrodires

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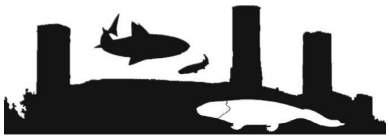
Arthrodira are the only placoderms in which teeth comparable to those of crown-group gnathostomes, with a bony base, mineralised crown, dentine, and a central pulp canal, have been confirmed (Rücklin *et al.,* 2012). The arthrodires from the Gogo Formation exhibit a wide variety of tooth morphologies (Long & Trinajstic, 2010) in different species, such as the unusual dentition of *Holonema* comprising a series of vertical tubes, the cusped toothplates of *Compagopiscis* and *Incisoscutum,* multidentate crushing toothplates of *Bullerichthyes* and shearing blades of *Eastmanosteus*. However an understanding of the underlying developmental mechanism that can explain the diversity in the arthrodire dentition is lacking (Johnason & Smith, 2005). Using a combination of synchrotron, micro-CT and traditional thin sectioning we demonstrate that although there are different tooth morphologies amongst taxa, arthrodires share a common tooth developmental model. We confirm the presence of resorption surfaces and remodelling within the toothplates and show how tooth morphologies differ in adults and juveniles, suggesting different feeding strategies depending on the life stage. The level of resorption present is dependent on the ontogenetic stage of the individual, being most evident in subadults and decreasing dramatically in older individuals in which the biting division of the infragnathal comprises mainly dermal bone, the teeth having being fully resorbed.

Johanson, Z. & Smith, M.M., 2005. Origin and evolution of gnathostome dentitions: a question of teeth and pharyngeal denticles in placoderms. – *Biological Reviews*, **80**(2): 303-345.

Long, J.A. & Trinajstic, K., 2010. The Late Devonian Gogo Formation lägerstatte of Western Australia: exceptional early vertebrate preservation and diversity. – *Annual Review of Earth and Planetary Sciences*, **38**: 255-279.

Rücklin, M., Donoghue, P.C., Johanson, Z., Trinajstic, K., Marone, F. & Stampanoni, M. 2012. Development of teeth and jaws in the earliest jawed vertebrates. – *Nature*, **491**(7426): 748-751.



Tracking Palaeozoic (mostly micro) fish Pt 2

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Thelodonts and early chondrichthyans especially have been the 'players' in my scientific career spanning five decades. New data on early vertebrates can be gleaned by examining the microfossils (ichthyoliths) they produce: scales (only in thelodonts), teeth, bones, spines, etc. and their histology and morphogenesis. Spines, "ichthyodorulites", have become a particular interest, and *Doliodus* and other early chondrichthyans offer a range of scale and spine types to consider in understanding the phylogeny of early gnathostomes. Finds of Silurian, Devonian and Carboniferous fossils from classic areas such as the Brown Clee Hill, Shropshire, S Wales, Norway, and eastern North America, include new agnathan and gnathostome remains, and those in peri-Gondwanan Poland, Iran, and Australia, and new areas, such as Idaho, Nevada, Morocco, Turkey, and Pakistan, provide not only new biostratigraphical data but palaeoenvironmental and palaeogeographical insights that are leading to a review of turiniid and other thelodonts (e.g. Hairapetian et al. 2016a, b, Turner et al. in press) as well as basal gnathostomes (e.g. Snyder et al. submitted).

Thelodont scales are not very abundant among Devonian fish microfossils from Poland, for instance (see poster Turner & Ginter 2017 this vol.); time to look for more. Much of the world still needs further investigation especially further back into the Ordovician. Many more 'eyes to the ground' are needed and time to stew up more rocks!

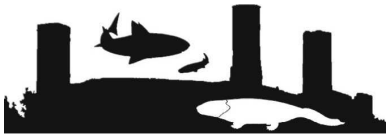
*Thanks to (among others) Bev Halstead (1933-1991), Alain Blieck, Henning Blom, Carole Burrow, Ted Daeschler, Humberto Ferron, Michał Ginter, the Göncüoglus, Vachik Hairapetian, Tiiu Märss, Ruth Mawson, Randy Miller, Mike Murphy, Daniel Snyder, John Talent, Peter Tarrant, Kate Trinajstic, Jo Vergoossen, Pat Vickers-Rich, Rod Williams, Ian Wilson (1943-1972), and Guy (1986-2012) and Tony Thulborn.

Hairapetian, V., Blom, H. and Turner, S. 2016a. Early Frasnian thelodont scales from central Iran and their implications for turiniid taxonomy, systematics and distribution. – *Journal of Vertebrate Paleontology*, 36 (4): e1100632.

Hairapetian, V., Roelofs, B., Trinajstic, K. and Turner, S. 2016b. Famennian survivor turiniid thelodonts of North and East Gondwana. *In*: Becker, R. T., Königshof, P. & Brett, C. E. (*Eds*) , Devonian Climate, Sea Level and Evolutionary Events. Geological Society, London, Special Publication 423, 273-289

Snyder, D. Daeschler, T Burrow, CJB, & Turner, S., 2017 sub. "*Gyracanthus" sherwoodi* (Gnathostomata, Gyracanthidae) from the Late Devonian of North America. Proceedings ANSP

Turner, S., Burrow, C. J.,, Williams, R. B. & Tarrant, P. 2017 in press. Welsh Borderland bouillabaisse: Lower Old Red Sandstone fish microfossils and their significance. In: Kendall, R. ed. *Lower Old Red Sandstone volume*, Brecon Meeting. *Proceedings of the Geologists' Association.*



New LORS microvertebrates (ichthyoliths) from the Welsh Borderland

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New microfossils of thelodonts, heterostracans, cephalaspids, anaspids and various gnathostomes (hereafter 'microvertebrates') have been found in the later Silurian and Lower Old Red Sandstone (LORS: Ludlow–early Emsian?) in the Welsh Borderland (Shropshire, Herefordshire, Worcestershire, Gloucestershire, and eastern Welsh counties) and South Wales. Many taxa, especially agnathan thelodont and acanthodian scales, have been known for over 150 years (Turner 1973, 1984, Vergoossen 1999, 2000) but only in recent studies have rarer elements been found (Turner et al. 2017 in press). New records include the youngest thelodonts in Britain and the first thelodont and acanthodian scales from Manorbier Bay, Pembrokeshire. Scales of acanthodian *Parexus recurvus* are barely distinguishable from those of stem chondrichthyan *Seretolepis elegans*. Simple 'radotinid' placoderm scales have been found. *Turinia pagei* as well as "*Nostolepis" robusta* are confirmed as key taxa for identifying the S/D boundary and changeover to Lochkovian fauna.

Vergoossen (1999) was the first to illustrate chondrichthyan remains, and our recent study has brought to light new material: placoid and polyodontode scales of basal sharks have been found and recognised in the Early Lochkovian Daugleddau Group (former "Ditton Gp") of the classic Brown Clee Hill district, Shropshire (e.g. Ball et al. 1961, Blieck & Tarrant 2001) and near Talgarth, Powys; chondrichthyan *Altholepis* is newly added to the faunal list. The presence of these widely distributed taxa adds to the debate on the sedimentological origins of the LORS deposits in the Welsh Borderland. Our finds extend the known range of several early sharks around the Old Red Sandstone continent, with further sharks recorded in southern Britain for the first time.

Ball, H.W., Dineley, D.L. and White, E.I. 1961. The Old Red Sandstone of Brown Clee Hill and the adjacent area. – *Bulletin of the British Museum (Natural History), Geology*, 5: 177 –310.

Blieck A. and Tarrant, P.R. 2001. *Protopteraspis gosseleti* (Vertebrata: Pteraspidimorphi: Heterostraci) from the Lower Devonian of Shropshire, England. – *Palaeontology*, 44: 95–112.

Turner, S. 1973. Siluro-Devonian thelodonts from the Welsh Borderland. – *Journal of the Geological Society, London*, 129(6): 557–584.

Turner, S. 1984. *Studies of Palaeozoic Thelodonti (Craniata : Agnatha)*. 2 vols. Unpublished Ph.D. thesis, University of Newcastle-upon-Tyne.

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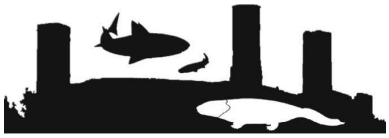
Vergoossen, J.M.J. 1999. Siluro-Devonian microfossils of Acanthodii and Chondrichthyes (Pisces) from the Welsh Borderland/south Wales. – *Modern Geology*, 24: 23–90.

Vergoossen, J.M.J. 2000. Acanthodian and chondrichthyan microremains in the Siluro-Devonian of the Welsh Borderland, Great Britain, and their biostratigraphical potential. – *In*: A. Blieck and S. Turner (Eds.), *Palaeozoic Vertebrate Biochronology and Global Marine/Non Marine Correlation, Final Report IGCP 328, 1991-1996. – Courier Forschungsinstitut Senckenberg*, 223: 175–199.



Middle Devonian thelodonts and associated fish from the Skały Formation, Holy Cross Mountains, Poland

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There are few records of mid to later Devonian thelodonts, the longest lived Palaeozoic agnathans (Märss *et al*. 2007, Hairapetian *et al*. 2016a, b). Sparse fish microremains have been found in limestones from the Middle Devonian (Upper Givetian) of the Skały Formation (Sierżawy Member), Świętomarz–Śniadka section, Łysogóry Region, northern Holy Cross Mountains (J. Kłossowski coll. 1976, see Kłossowski 1985; Woroncowa-Marcinowska 2012). The fish remains are associated with conodonts of *hemiansatus* to *ansatus* Zones. Three thelodont scales came from Świętomarz village, Bodzentyn syncline and Woroncowa-Marcinowska (2012, fig. 6F-O) figured ichthyoliths including one thelodont head scale (6H), acanthodian (6F, I, L-M), possible placoderm (6K) and an osteichthyan lepidotrichium (6O).

Based on the fragile crowns with spinelets and thin bases with small tuberosities, the thelodont scales are referred to the genus *Australolepis* Turner & Dring, 1981. The scales are more elongate and spiny than those of the late Givetian to Frasnian type species *A. seddoni* and so a new species is probable but more material is needed to see the variation.

This is the first record of a mid-Devonian thelodont from Poland. The find extends the geographic range of *Australolepis* from East Gondwana (Western Australia: Turner & Dring 1981, Turner 1997, Hairapetian *et al.* 2016b) and north Gondwana shoreline (Iran: Turner *et al.* 2002, Hairapetian *et al*. 2016a) further around Palaeotethys.

Hairapetian, V., Blom, H. & Turner, S. 2016a. Early Frasnian thelodont scales from central Iran and their implications for turiniid taxonomy, and their implications for turiniid taxonomy, systematics and distribution. – *Journal of Vertebrate Paleontology* **36** (3): e 1100632 (17 pp).

Hairapetian, V., Roelofs, B., Trinajstic, K. & Turner, S. 2016b. Famennian survivor turiniid thelodonts of North and East Gondwana. – *In*: Koenigshof, P. (*Ed.*), *Devonian Change: Case studies in Palaegeography and Palaeoecology*. *Geological Society of London Special Publication* **423,** 273-289.

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Märss, T., Turner, S., Karatajute-Talimaa, V. 2007 Agnatha II - Thelodonti. Volume **1B**. – *In*: Schultze H-P. (*Ed.*) *Handbook of Palaeoichthyology*. *Verlag Dr Friedrich Pfeil*, Munich, 143 pp.

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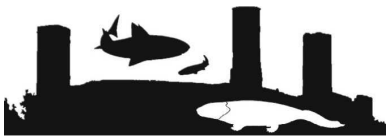
Turner, S. & Dring, R. 1981. Late Devonian thelodonts from the Gneudna Formation, Carnarvon Basin, Western Australia. – *Alcheringa* **5**: 39-47.

Turner, S., Burrow, C. J., Gholamalian, H. & Yazdi, M. 2002. Late Devonian (early Frasnian) microvertebrates and conodonts from the Chahriseh area near Esfahan, Iran. – *Memoirs of the Association of Australasian Palaeontologists* **27**: 149-159.

Woroncowa-Marcinowska, T., 2012. Middle Devonian conodonts and structural implications for Świętomarz – Śniadka section (Holy Cross Mountains). – *Annales Societatis Geologorum Poloniae* **82**: 349-360.



The unique diversity of basal placoderms from the Prague Basin (Czech Republic); their phylogenetic and evolutionary implications

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Our new investigation of the Prague Basin Lochkovian and Pragian placoderm fauna has finally resolved the long prevailing confusion about the variable character states in individual taxa, especially the genus *Radotina* as described by Gross (1950, 1958, 1959). Five genera (*Radotina*, *Tlamaspis*, *Sudaspis, Holopetalichthys* and *Kosoraspis*) were proven valid or established based on well documented unique characters of skull roof patterns and cranial morphology (Vaškaninová & Ahlberg 2017).

The reinterpreted *Radotina* has a skull roof with large tesselated areas separating the macromeric bones. The new genus *Tlamaspis* has an extremely elongated facial region and a dermal skull roof lacking tesserae between the centrals and nuchal. The other new genus *Sudaspis* has a long prenasal region with a distinctive, stepped lateral profile. The taxonomic distinctness of the enigmatic genus *Kosoraspis* is not in dispute. All these taxa can be included among the acanthothoracids based on the presence of a projecting "upper lip", a feature that may, however, be primitive for jawed vertebrates (Dupret et al. 2014). Their detailed investigation could add substantially to the discussion about early gnathostome cranial evolution as well as the evolution of dermal bone macromery.

We have also resolved the taxonomic confusion following the generic determination of the so called *´Radotina´ prima* (previously known as *Coccosteus primus*, *Holopetalichthys novaki* and *Radotina tuberculata*) and its problematic position within the acanthothoracids. We establish the name combination *Holopetalichthys primus* (Barrande, 1872). The genus *Holopetalichthys* is excluded from the acanthothoracids on the basis of the probable absence of the prenasal area and typical features in its dermal skeleton.

Preliminary results from the synchrotron tomography investigation of the Prague Basin Lower Devonian placoderms confirm the proposed taxonomy. We consider all the previously published attempts to reconstruct or interpret the ´radotinid´ material, apart from references to holotypes, as invalid because they inadvertently combine information from more than one taxon.

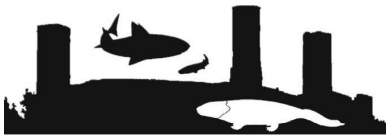
Dupret, V., Sanchez, S., Goujet, D., Tafforeau, P. & Ahlberg, P.E. 2014. A primitive placoderm sheds light on the origin of the jawed vertebrate face. – *Nature*, **507**: 500-503.

Gross W. 1950. Die paläontologische und stratigraphische Bedeutung der Wirbeltierfaunen des Old Reds und der marinen altpaläozoischen Schichten. – *Abhandlungen der Deutschen Akademie der Wissenschaften zu Berlin. Mathematisch-naturwissenschaftliche Klasse*, **1**: 1-130.

Gross W. 1958. Über die älteste Arthrodiren-Gattung. – *Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden*, **86**: 7-30.

Gross W. 1959. Arthrodiren aus dem Obersilur der Prager Mulde. – *Palaeontographica Abteilung A*, **113**: 1-35.

Vaškaninová, V. & Ahlberg, P.E. 2017. Unique diversity of acanthothoracid placoderms (basal jawed vertebrates) in the Early Devonian of the Prague Basin, Czech Republic: A new look at *Radotina* and *Holopetalichthys*. – *PLoS ONE*, **12**: e0174794.



Unexpected dentitions discovered in three genera of Early Devonian acanthothoracid placoderms from the Prague Basin (Czech Republic)

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Acanthothoracid placoderms are probably among the most primitive jawed vertebrates (Dupret et al. 2014), and could thus be informative about the origin of jaws and teeth. Only two supposed acanthothoracid dental elements have been described: one (Goujet & Young 2004, Fig. 3A) may not belong to an acanthothoracid and the other, an isolated element (Rücklin & Donoghue 2015), is probably a dermal tessera (Burrow et al. 2016).

In the course of investigating acanthothoracid material from the Lower Devonian of the Prague Basin by synchrotron microtomography, we have discovered well-preserved dentitions in the genera *Kosoraspis*, *Radotina* and *Tlamaspis* that differ fundamentally from the published examples. The teeth of *Kosoraspis* grow on long, narrow bones with transversely concave basal surfaces. At least six elements can be attributed to one individual. The teeth are arranged in transverse files, gradually enlarging towards the lingual side. The bones have no distinct facial laminae, but appear to have been located immediately adjacent to the jaw margin. In *Radotina*, a posterior supragnathal is preserved in articulation on the palatoquadrate complex. It is a long, slender bone, carried by the suborbital rather than the palatoquadrate and located immediately inside the jaw margin. The teeth are blade-like, resembling the odontodes on the edges of the dermal tesserae of *Radotina*, and are arranged in alternating tooth files. The tooth-bearing bones of *Tlamaspis* (a new genus, previously included in *Radotina*; Vaškaninová & Ahlberg 2017) are marginal elements with a deep facial lamina; this lamina carries 3-4 rows of odontodes near the jaw margin, the most marginal row taking the form of large, well-spaced conical teeth. These dentitions bear no resemblance to those of arthrodire placoderms, but share characteristics with those of primitive osteichthyans and chondrichthyans. They will have a major impact on our understanding of dental evolution. A premedian plate from the Prague Basin that is probably attributable to the non-acanthothoracid *Holopetalichthys* (Vaškaninová & Ahlberg 2017) closely resembles the one associated with the "acanthothoracid" dentition of Goujet and Young (2004). This suggests an

alternative identity for the latter and may explain why it differs greatly from the dentitions described here.

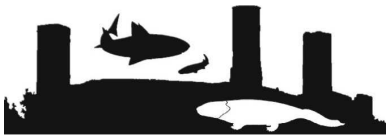
Burrow, C., Hu, Y. & Young, G. 2016. Placoderms and the evolutionary origin of teeth: a comment on Rücklin & Donoghue (2015). – *Biology letters*, **12**: 20160159.

Dupret, V., Sanchez, S., Goujet, D., Tafforeau, P. & Ahlberg, P.E. 2014. A primitive placoderm sheds light on the origin of the jawed vertebrate face. – *Nature*, **507**: 500-503.

Goujet, D. & Young, G.C. 2004. Placoderm anatomy and phylogeny: new insights. – *In:* G. Arratia, M.V.H. Wilson, R. Cloutier (*Eds.*), *Recent Advances in the Origin and Early Radiation of Vertebrates*, pp. 109-126. *Verlag Dr. Friedrich Pfeil,* München.

Rücklin, M. & Donoghue, P.C.J. 2015. *Romundina* and the evolutionary origin of teeth. – *Biology letters*, **11**: 20150326.

Vaškaninová, V. & Ahlberg, P.E. 2017. Unique diversity of acanthothoracid placoderms (basal jawed vertebrates) in the Early Devonian of the Prague Basin, Czech Republic: A new look at *Radotina* and *Holopetalichthys*. – *PLoS ONE*, **12**: e0174794.



Late Devonian ichthyoliths from the Ostrówka Quarry in the Holy Cross Mountains, Poland

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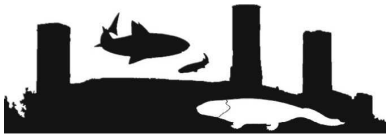
The late Famennian section of the Ostrówka Quarry shows a well-documented process of drowning of the carbonate platform formed in the Middle Devonian and fragmented during the end of this period (Szulczewski et al. 1996). In the section the last episode of the submersion is recorded and characterized by the stratigraphic condensation and big amount of various invertebrate and vertebrate remains (ichthyoliths; Ginter, 1990) deposited in deep-water conditions.

Recent study focuses on fish macro- and microremains regarding stratigraphy based on conodonts. Among vertebrates, chodrichthyans and acanthodians assemblage have been ascertained. Shark teeth dominate in the studied material and show few forms of phoebodontids (*Phoebodus* and *Thrinacodus*). *Ctenacanthus* cf. *major* is represented by fragments of fin-spines. One of them probably reached more than 70 cm length. Acanthodians are represented by dozens of scales unidentified yet, but also by the ischnacanthid lower jaw broadly similar to the *Atopacanthus*.

Detailed description of the entire assemblage of fishes remains will importantly contribute to our knowledge on Famennian vertebrate community in the Holy Cross Mountains.

Ginter, M. 1990. Late Famennian shark teeth from the Holy Cross Mts, Central Poland. *Acta Palaeontologica Polonica*, **40**, 69-81.

Szulczewski, M., Belka, Z., & Skompski, S. 1996. The drowning of a carbonate platform: an example from the Devonian-Carboniferous of the Holy Cross Mountains, Poland. *Sedimentary Geology*, **106**, 21-49.



Devonian Vertebrates from Peru (Titicaca lake, Puno)

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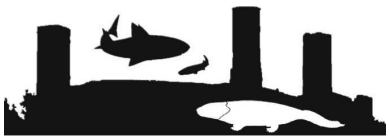
Despite the relative worldwide abundance of Siluro-Devonian vertebrates, those are very rare in the South American continent. According to Janvier & Maisey (2010), the fossil record of South American Devonian vertebrates is limited to two faunal associations: an Lower Eifelian-Frasnian placoderms and osteocthyan dominated assemblage in the northwest of the continent (Venezuela and Colombia); and a second Lochkovian-Eifelian assemblage represented mainly by chondrichthians and acanthodinamd situated south to the present-day equator (Bolivia and Brazil). Besides those countries (and with the exception of the Falkland Islands remains) there are so far no other reports of Devonian vertebrates in the South American continent. Thus, every new finding is important for a better understanding of the early vertebrates communities that inhabited the lower and middle Devonian seas of the southwest margin of Gondwana,

In this work, we describe a new locality of Devonian vertebrates remains from Peru. The material show in the present work was recovered from the Chagrapi Formation, Silurian-Devonian in age (Newell, 1949), in the Puno region, located in the southeastern Peruvian territory, on the shores of Titicaca Lake. Specimens were found in noduls and scanned with a Nikon XT H 225 industrial CT. Two studied specimens represent parts of the mandibular arch attributed to the chondrichthyan *Pucapampella*, and the third specimen was assigned to a fin plate of *Zamponiopteron.* So far, both *Pucapampella* and *Zamponiopteron* had been described in the Middle Devonian of Bolivia (Janvier & Suárez-Riglos, 1986); and *Pucapampella* in the Middle Devonian of South Africa (Anderson *et al.,* 1999), a geographically close regions during this period. In this sense, the joint presence of both taxa defines a unique and interesting ichthyological association in the Southern Hemisphere, the *Pucapampella-Zamponiopteron* community, characterized by a high relative abundance of chondrichthyan in comparison with other regions of the northern Hemisphere, as seen in Europe (Janvier & Maisey, 2010). These finding indicate the potential of the Peruvian rocks for the discovery of new early vertebrates in the South American continent. They are not only the first Devonian vertebrates from Peru but also the first Paleozoic ones, being significant for a developing paleontology in the country.

This work has been founded by the Spanish Research Project CGL2014-52662-P and by the Generalitat Valenciana Research Project GV/2016/102.

Anderson, M. E., Almond, J. E., Evans, F. J., & Long, J. A. 1999. Devonian (Emsian-Eifelian) fish from the Lower Bokkeveld Group (Ceres Subgroup), South Africa. – *Journal of African Earth Sciences*, **29**:179-193.

Janvier, P. & Suarez-Riglos, M. 1986. The Silurian and Devonian vertebrates of Bolivia. – *Bulletin de l'Institut français d'Études andines*. **15**: 73-114.
Janvier, P. & Maisey, J.G. 2010. The Devonian vertebrates of South America and their biogeographical relationships. – *In: Elliott et al. (Ed.), Morphology, Phylogeny and Paleobiogeography of Fossil Fishes*, pp. 431-459. Verlag Dr. Friedrich Pfeil ,München.
Newell, N.D. 1949. Geology of the lake Titicaca region, Peru and Bolivia. – *Geological Society of America Memoirs,* **36**: 1-124.



The subdivision and correlation of the Silurian fish-bearing strata in Northwest Hunan, China

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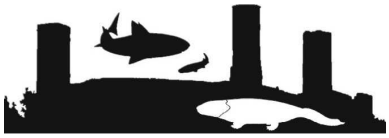
The Silurian strata in Northwest Hunan, China yield the galeaspids *Dayongaspis*, *Konoceraspis*, *Dunyu*, the chondrichthyans *Sinacanthus*, *Neosinacanthus*, *Hunanacanthus*, *Eosinacanthus*, *Tarimacanthus*, and the placoderms *Shimenolepis* and "*Wangolepis*" (Zhao & Zhu, 2010, 2014; Zhao *et al*., 2016). The antiarch *Shimenolepis* from the site around the Shanmen Reservoir in Lixian County, Hunan, has long been regarded as the oldest known placoderm (dating Telychian of Llandovery) in the world (Wang, 1991).

Since 2008, we have conducted a series of extensive field investigations and excavations in the Silurian marine deposits of Northwest Hunan. Some new findings of Silurian fishes including maxillate placoderms in Northwest Hunan provide additional evidence on the study of the Silurian stratigraphy. The Silurian fish-bearing strata in Northwest Hunan can be subdivided into the Rongxi, Huixingshao, and Xiaoxi formations in ascending chronological order, which can be correlated with the Lower Red Beds, the Upper Red Beds, and the Ludlow Red Beds in South China respectively (Rong *et al.*, 2012; Zhao & Zhu, 2014, 2015; Zhao *et al*., 2016). A new look at the Silurian strata in Lixian suggests that the age of *Shimenolepis* is Late Ludlow rather than Late Llandovery as previously suggested (Wang, 1991; Zhao *et al*., 2016). The research on Silurian biostratigraphy and fishes in Northwest Hunan not only provides critical data in the quest for the morphology and systematics of early gnathostomes, but also offers new paleoichthyological evidence for the subdivision, correlation, and age assignment of Silurian marine red beds in South China.

Rong, J.-Y., Wang, Y. & Zhang, X.-L. 2012. Tracking shallow marine red beds through geological time as exemplified by the lower Telychian (Silurian) in the Upper Yangtze Region, South China. – *Science China: Earth Sciences*, 42: 862-878.
Wang, J.-Q. 1991. The Antiarchi from the Early Silurian of Hunan. – *Vertebrata PalAsiatica*, **29**: 240-244.
Zhao, W.-J. & Zhu, M. 2010. Siluro-Devonian vertebrate biostratigraphy and biogeography of China. – *Palaeoworld*, **19**: 4-26.
Zhao, W.-J. & Zhu, M. 2014. A review of the Silurian fishes from China, with comments on the correlation of fish-bearing strata. – *Earth Science Frontiers*, **21**: 185-202.

Zhao, W.-J. & Zhu, M. 2015. A review of Silurian fishes from Yunnan, China and related biostratigraphy. *Palaeoworld*, **24**: 243-250.
Zhao, W.-J., Zhu, M., Liu, S., Pan, Z.H. & Jia, L.-T. 2016. A new look at the Silurian fish-bearing strata around the Shanmen Reservoir in Lixian, Hunan Province. – *Journal of Stratigraphy*, **40**: 349-358.



New data from the Silurian Xiaoxiang Fauna, a window to display the early radiation of jawed vertebrates

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During the past decade, inspiring discoveries of early vertebrates have been known from the Silurian Xiaoxiang Fauna (Late Ludlow, about 423 million years ago), a valuable and rare window to display the early evolution of gnathostomes. They include galeaspid *Dunyu longiforis* (Zhu *et al*., 2012), maxillate placoderms *Entelognathus primordialis* (Zhu *et al*., 2013) and *Qilinyu rostrata* (Zhu *et al*., 2016), and osteichthyans *Guiyu oneiro* (Zhu *et al*., 2009), *Megamastax amblyodus* (Choo *et al.,* 2014) and *Sparalepis tingi* (Choo *et al*., 2017). These findings yielded unprecedented mix of characters for inferring the sequence of character transformation at the placoderm-osteichthyan transition, and at the root of jawed vertebrates in general, thus challenging earlier assumptions and even some of deeply entrenched views about the homology and phylogeny of early gnathostomes. Along with the successive field collection in the Kuanti Formation of Qujing, Yunnan, rich new fossils including a dozen articulated specimens, have been found to display an unexpected high diversity and morphological disparity of early gnathostomes, and push the radiation of jawed vertebrates well before the advent of the Devonian period. Here I will show some new data of these findings based on high-resolution CT scanning, which might constitute a challenging and rewarding opportunity to bring about new breakthroughs in the study of early vertebrate evolution.

Choo, B., Zhu, M., Qu, Q.-M., Yu, X.-B., Jia, L.-T., & Zhao, W.-J., 2017. A new osteichthyan from the late Silurian of Yunnan, China. - *PLoS One*, **12**: e0170929.
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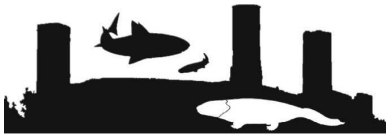

The endocast of an exceptionally preserved 400 myr placoderm, and evolution of the central neural system in stem gnathostomes

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Placoderms are basal jawed vertebrates that were dominant in the Devonian 'age of fishes'. New evidence from Chinese Silurian 'maxillate placoderms' (Zhu et al., 2013, 2016) suggests that they form a paraphyletic basal array of groups in the gnathostome stem (Zhu et al., 2013, 2016). Previously they were regarded as monophyletic monophyletic (Denison, 1978; Goujet and Young, 2004; Young, 2010). As a paraphyletic stem group, their character combinations will be pivotal in the understanding of gnathostome ancestral conditions, so comprehensive and detailed investigation of their morphology is important.

Placoderms are mostly preserved as isolated skulls and dermal plates. Sometimes the ossified internal skeleton is preserved (e.g. isolated braincases). Here we report recent progress on an articulated Early Devonian buchanosteid arthrodire from Burrinjuck, SE Australia (Young et al., 2001), one of the best preserved early placoderms to date. It has a complete perichondrally ossified braincase and articulated rostral and optic capsules, jaws, cheek and opercular unit. The intra-cranial morphology has been segmented and dissected 3-dimensionally, revealing exquisite detail of the spacial relationship between the central nervous system, the circulation system and skeletal units.

Recent documentation of "maxillate placoderms" shows that they display similarities to both osteichthyan and placoderm taxa, more specifically arthrodires (Zhu et al., 2013). Maxillate placoderms are resolved as more crownward than other placoderm subgroups and thus highly relevant to the origin of modern jawed vertebrates. Study on the neurocranium of *Entelognathus* is still preliminary. The comparisons with the buchanosteid specimen will provide new information on neurocranial character transitions from basal to crownward stem gnathostomes.

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Field excursions – descriptions of stops

PIOTR SZREK

Stop 1

Zachełmie Quarry Reserve – the first tetrapod track-bearing locality

The Zachełmie quarry near Kielce (180 km S of Warsaw) is well known to most Polish and foreign paleontologists because of the occurrence of the oldest tetrapods trackways and footprints. Discovery and description of this phenomena (Niedźwiedzki et al., 2010) has made this locality one of the most recognizable geological site in Poland. Until this moment Zachełmie was known to Polish geologists because of its highly visible Variscan angular unconformity between the emerging grey Devonian dolomites and classical red formations of the Permian and Triassic periods. Recently the quarry draws in geology field trips from universities across the country and abroad.

Zachełmie is the abandoned quarry which is a natural reserve (from 2010). It is located in the northwestern part of the Holy Cross Mountains and exposes about 100 m of the Middle Devonian strata covered with about 10-11 m thick Permian-Triassic deposits. The Devonian part of the section comprises the upper part of the marginal marine Wojciechowice Formation and its contact with the overlying marine Kowala Formation. The lower unit is composed of thin- to medium bedded, micritic dolomite mudstones and wackestones with a variable admixture of clayey material, interlayered with dolomitic marls and shales.

The Wojciechowice Formation represents a unique episode of restricted, extremely shallow-water carbonate sedimentation within the generally open marine marly carbonate and, subordinately, siliciclastic deposition that prevailed during the Middle Devonian in the northern Holy Cross Mountains. The lower, trackway-containing part of this formation, almost devoid of other fossils, contains abundant laminites with desiccation cracks and raindrop impressions and seems to represent an extremely shallow marine tidal, perhaps lagoonal, environment. Recent studies pointed that the Wojciechowice Formation were attributed to shallow marine tidal-flats (Niedźwiedzki et al., 2010) or marine non-tidal shallow lagoons separated from an open marine basin by sparsely vegetated islands and spits (Narkiewicz & Retallack, 2014; Narkiewicz et al., 2015).

The Kowala Formation shows deeper environment of the open sea developed on the carbonate platform. It is almost completely devoid of trace-fossils in favor of body-fossils of marine invertebrates (sponges, brachiopods, crinoids). This part of the section includes pure, crystalline dolomites with amphiporoid biostromes (see Narkiewicz & Narkiewicz, 2010 and Narkiewicz et al., 2015).

Latest studies of the Devonian part of the section revealed new, more precise data in environment and paleontology considerations – for details see the article by Niedźwiedzki *et al.* in this volume.

The Buntsandstein deposits consist of red and brown conglomerates, sandstones and mudstones that overly, unconformity surface of the karstified Devonian carbonates. The early Triassic age corresponds to magnetostratigraphic research carried out by Nawrocki *et al.* (2003) and the latest Permian may be supported by conchostraca found by Ptaszyński and Niedźwiedzki (2004). The lower part of the succession is related to marine succession system deposited during transgressive phase. The upper part represents environments of braided rivers. Big amount of vertebrate tracks ichnotaxa has been described from Zachełmie

(Ptaszyński & Niedźwiedzki, 2005, 2006). They represent mostly various amphibian and reptiles animals.

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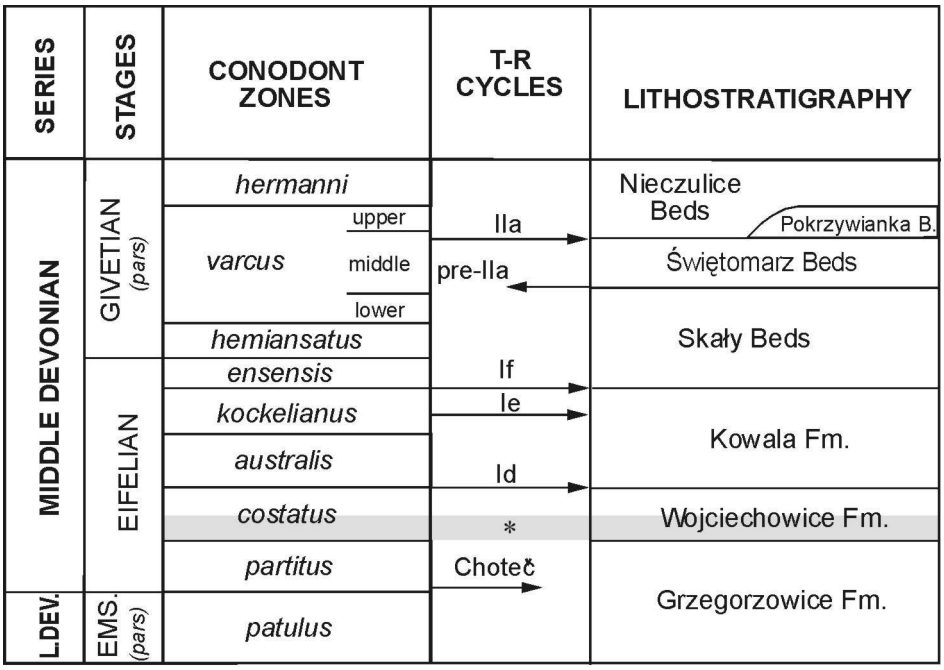

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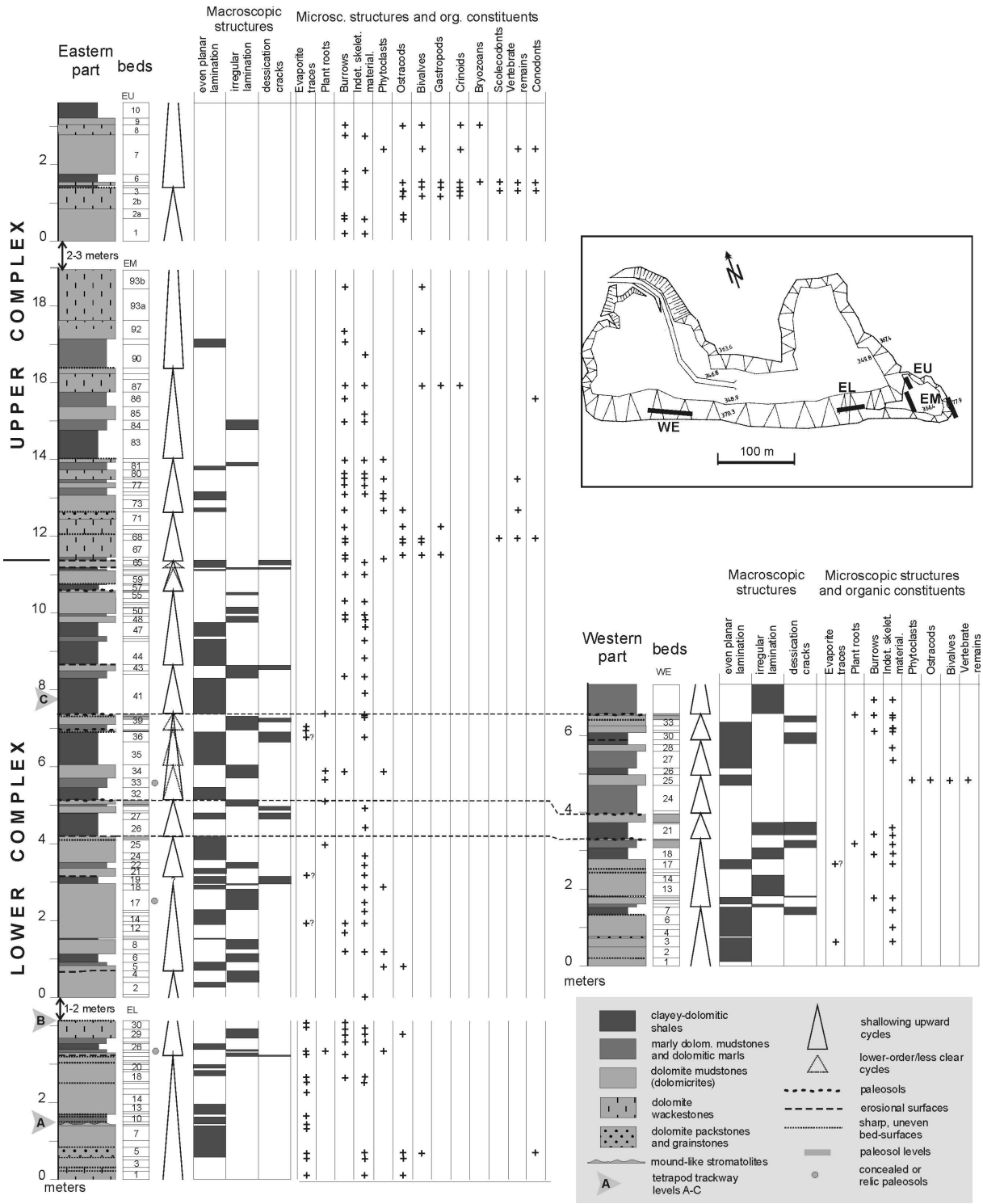

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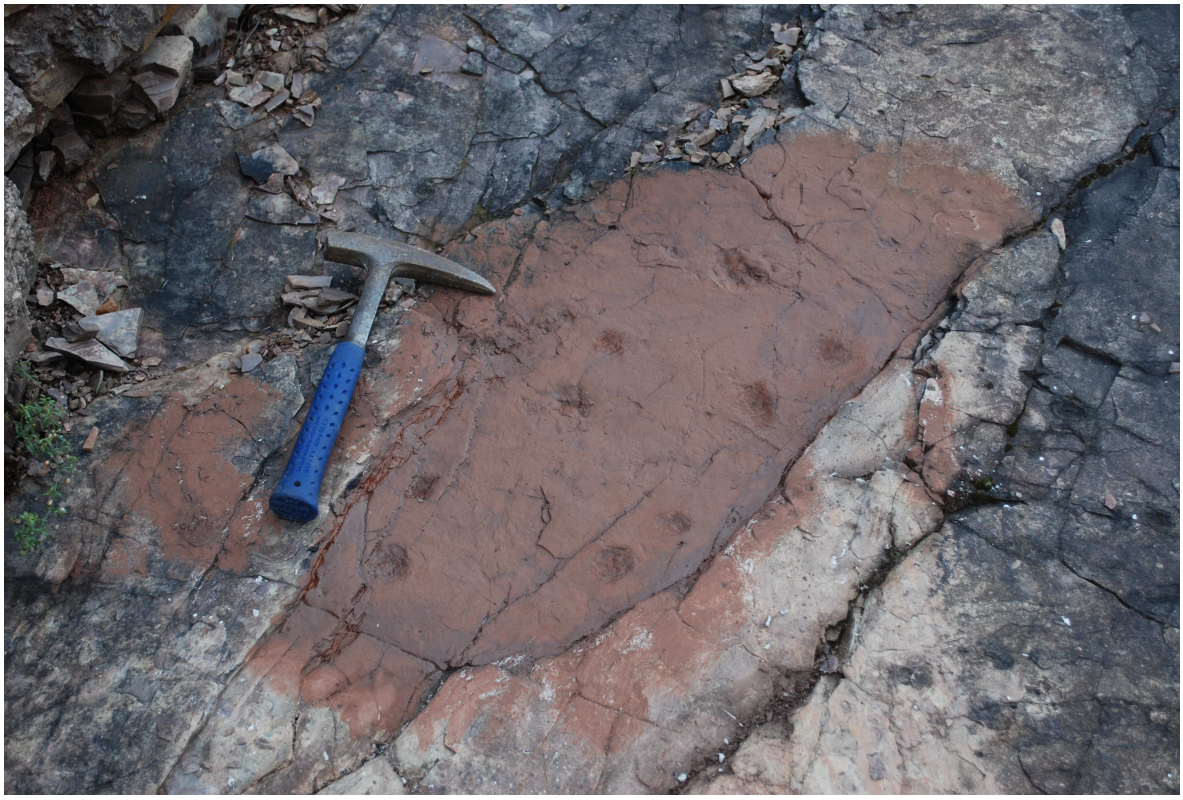
Figures

1. Stratigraphic framework of the Eifelian in the northern part of the Holy Cross Mountains with indicated position of the studied Zachełmie section (after Narkiewicz and Narkiewicz 2010 and Narkiewicz et al. 2015).
2. Detailed graphic log of the studied section (after Narkiewicz et al. 2015).
3-4. Tetrapod trackways. Specimens removed from the quarry to the museum.
5. Tetrapod footprints with finger imprints well visible.



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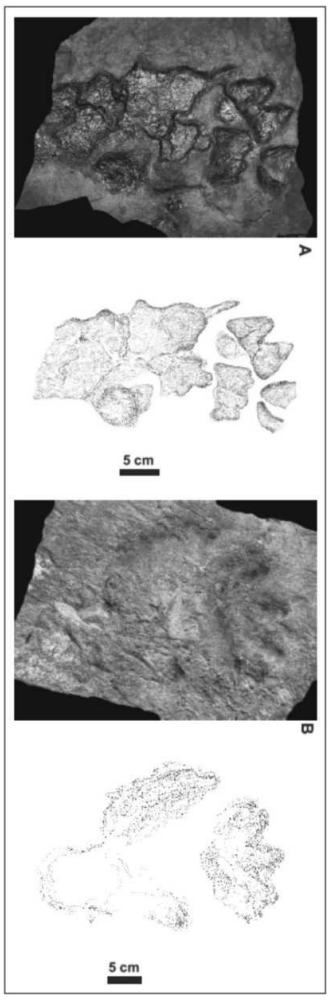

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Stop 2

Castle Hill (Góra Zamkowa) at Chęciny

The hill, situated in the southern part of the town of Chęciny, is crowned by the ruins of a 13th century castle built by a Polish king, probably Władysław Łokietek. Geologically, the hill is located in the southern limb of the Chęciny Antycline which is the westernmost structure of Palaeozoic core of the Holy Cross Mountains. The middle part of this structure, built of Cambrian clastic rocks (shales and thin-bedded sandstones) forms a wide valley. This is one of the best examples of the inverted relief. There is a gap between the Cambrian and the Devonian; the discordance between the Cambrian and Lower Devonian deposits measured in this part of the Holy Cross Mountains reaches 40 to 70°. The hill is built up of carbonate rocks, dolomites and limestones, of the Givetian and Frasnian age. The younger part of the section, with limestone deposits, is exposed in a small quarry and a few outcrops located on the slopes.

The best for observation is the quarry located on the western slope of the hill ("Western Quarry"), below the castle. Activity of the quarry started together with the castle foundation and continued with interruptions until the World War II. One of the best-known section of the Kowala Formation is exposed in this site. A few sets of carbonate rocks were distinguished in this section (Racki 1993): stromatoporoid-amphiporoid limestones, grained limestones with brachiopods and coral debris, thick bedded limestones with echinoderms, brachiopods and gastropods, and a complex of thin layers of limestones with cherts. The total thickness is about 50 m.

At the foot of the slope, marly shales and thin-bedded limestones of the Frasnian age are exposed. Farther to the south these deposits are covered with Permian conglomerates and Lower Triassic red clays and sandstones (Buntsandstein).

The fissures in the Devonian limestones are filled by hydrothermal mineralization (copper-polymetallic and Pb-Zn ores with barite) of both the Variscan and Alpine age (Rubinowski 1962). These vein infillings were mined in the 16th and 17th century on the northern slopes of the Castle Hill.

Rubinowski, Z. 1962. Outline of Metallogeny in the Paleozoic Strata of the Holy Cross Mountains. *Geological Review*, **8**.

Rubinowski, Z. 1968. Observation Site at Góra Zamkowa near Chęciny. – *In*: The Palaeozoic and Mesozoic in the Świętokrzyskie Mts. and the Cainozoic in the Carpathian Foredeep. *International Geological Congress, Prague 1968*. Warsaw.

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Stop 3

Wietrznia Quarry in Kielce

Wietrznia is an abandoned quarry closed in 1984 where Frasnian limestones and Fammenian shales have been exploited for the last century. It is located in the south-eastern part of the city of Kielce and in the easternmost part of the Kadzielnia Chain which is formed of Upper Devonian carbonate rocks. It belongs to the western part of a bigger geological structure – the Kielce-Łagów Synclinorium. In the Wietrznia Quarry the Middle Devonian (Givetian) dolomites and limestones also were excavated. Wietrznia was a mountain until the mining activity turned it in a 30 m deep hole (Fig. 1).

This place has a long, more than a hundred-year history of geological researches but the first complete description was given by Szulczewski in 1971. In the lower (western) part of the section (Pl. 2, Fig. 1), transitional reef-to-basin Frasnian deposits dominate. They are mainly composed of laminated or graded micritic limestones, nodular limestones, and detrital limestones. These rocks contain a large number of diverse fossils. Among others, there were noted brachiopods, gastropods, bivalves, rugose corals, stromatoporoids, and one of the best assemblages of vertebrates in the Holy Cross Mountains. The latter consists of ptyctodonts, arthrodires, porolepiforms, dipnoans, coelacanths and sharks (Gorizdro-Kulczycka 1934, 1950, Kulczycki 1957, Liszkowski & Racki 1993, Ginter 1994, Ivanov & Ginter 1997, Ginter 2004, Szrek 2007).

The synsedimentary block tectonics (Fig. 2) caused a variety of marine environments in this small area, mainly during the later part of the Frasnian and the earliest Famennian (Szulczewski 1971). The succession shows progressing, stepwise submersion of the carbonate platform. During that time, the carbonate platform was broken and by the middle Famennian sedimentation in the most of the Kielce area became uniform, except for isolated places. The last Devonian member in the Wietrznia Quarry, marls, marly shales and shales (Pl. 2, Fig. 2) similar to the Łagów Beds in the eastern part of the Holy Cross Mts, began in the Middle *Palmatolepis crepida* conodont Zone.

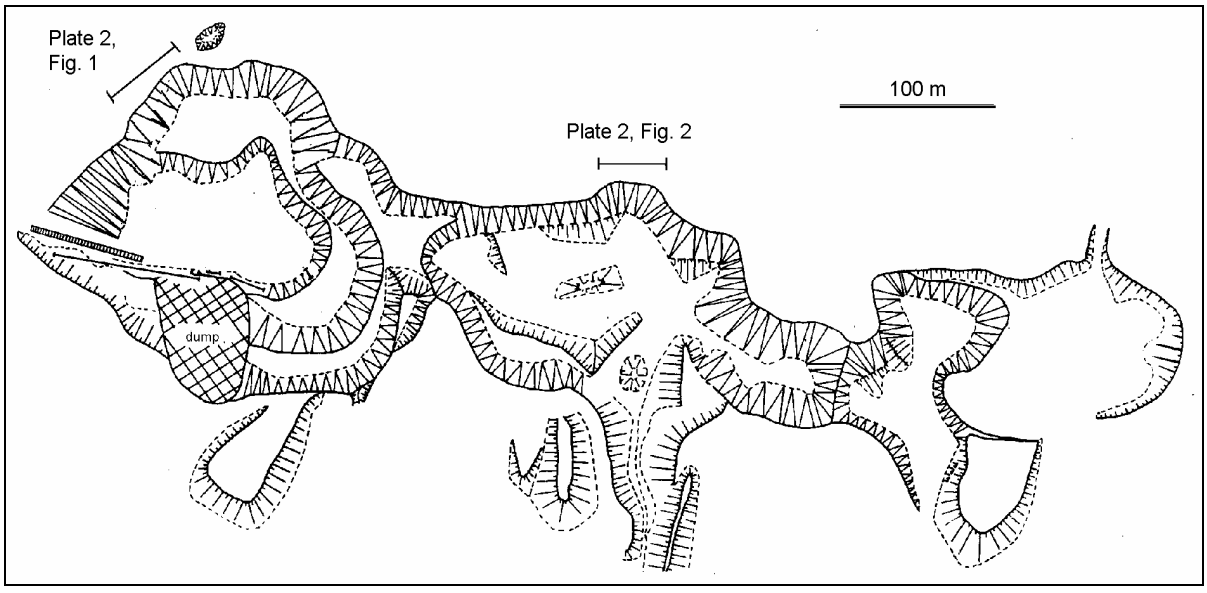

Fig. 1. Sketch view of the Wietrznia Quarry in Kielce (after Racki 1993, modified).
Note the positions of parts illustrated in colour plates.

Now the quarry is a protected area, a Geological Reserve named after Zbigniew Rubinowski who was a very meritorious geologist from Kielce.

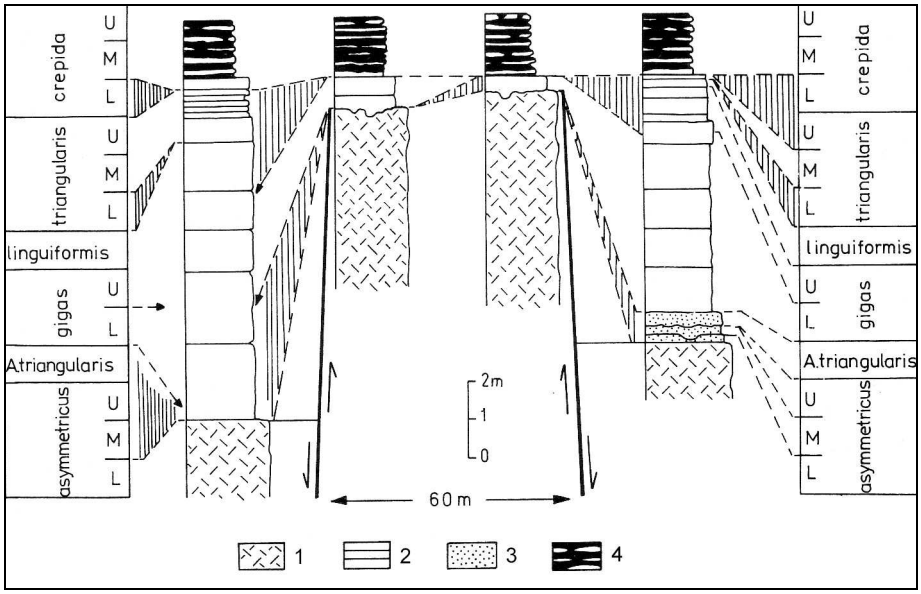

Fig. 2. Blocks in the Wietrznia Quarry, caused by synsedimentary tectonics. 1 – massive biohermal limestones, 2 – micritic pelagic limestones, 3 – organodetritic grainstones, 4 – marls and shales. From Szulczewski (1989).

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Stop 4

Ujazd

The outcrop is located in the small village Ujazd near Iwaniska, near the NW-SE road from Iwaniska to Staszów, in the central part of the Holy Cross Mountains, about 190 km south of Warsaw. It is the small abandoned quarry described in details by Szrek *et al.* (2016), where sandstone was exploited for local needs.

The Lower Devonian at Ujazd can be observed in a series of small exposures of white quartzite sandstones. These sandstones were last exploited by local residents more than 30 years ago. Recently, the exposures have become almost completely overgrown by plants, partly in a forest. One of those outcrops was re-investigated between 2011 and 2014.

The section studied in detail is about 4 m thick. It is composed of 1–2 m-thick sandstone beds interbedded with tuffaceous claystone layers that are up to 20 cm thick (Fig. 3). The strata dip about 20° to the north and maintain a strike of about 30°E. This section represents a very shallow water, low-energy marine environment. Petrographic and sedimentological investigations of the lower part of the exposed section indicate the backshore or nearshore. The upper part was formed in relatively stable conditions, but two well visible, wide but shallow, sandstone-filled channels occur here, suggesting a local erosional event. In the locality, some rare and rather poorly preserved vertebrate fossil remains were collected, representing sarcopterygians and placoderms that correspond to the fish assemblage from the Podłazie locality (Szrek et al., 2014). Lithostratigraphic considerations suggest that sandstones exposed at Ujazd belong to the lower part of the Winna Formation (Fijałkowska-Mader & Malec, 2011). Rare occurrences of the invertebrate trace fossils *Lockeia, Monomorphichnus,* and *Rhizocorallium* at the Podłazie locality suggest the *Cruziana* ichnofacies. The same ichnofacies is probably present in the locality studied. This may indicate a shallow marine, sandy but protected environment, such as, e.g., a flood-tidal delta in a lagoon, but limited exposure does not permit us to test this hypothesis.

The fish feeding traces occur on two relatively well exposed surfaces in the northern and western part of the outcrop. The lower surface, A, was recognized on the top of a 1 m-thick sandstone bed. The higher surface, B, is at the top of a 0.5 m-thick sandstone bed which is covered by a thicker tuffaceous claystone layer. Both sandstone beds are composed of fine-grained quarzitic white sandstone. They are structureless, although poorly preserved lamination and mudstone intraclasts are locally visible, mainly in the lower sandstone bed. The trace fossil discussed is preserved as concave epichnia that share the same morphology, size and state of preservation. Both surfaces are covered with tuffaceous claystone.

Traces from Ujazd are the oldest evidence of the ichnogenus *Osculichnus* Demírcan *et* Uchman, 2010, which has been known mostly from hypichnia so far. *Osculichnus tarnowskae* – a new species name for traces from Ujazd – is interpreted as a hunting trace of a fish intruding its mouth into the sediment. The trace makers probably belong to one genus. The basic morphological details, including the U-shaped and/or trapezoidal shape of the mouth, the probable presence of tuberculate tooth-plates, and the imprints of folding skin, point to a short-snouted dipnoan fish with a head morphology broadly similar to *Dipnorhynchus* or *'Chirodipterus' australis*. In a few specimens, the snout shape is preserved almost perfectly, as confirmed by a 3D reconstruction based on laser scans.

Osculichnus tarnowskae is the oldest feeding trace produced by a dipnoan fish and the first direct evidence for Early Devonian dipnoan feeding behaviour, as well as the first record of their three-dimensional soft-tissue morphology such as lips.

The discovery of *Osculichnus tarnowskae* and other trace fossils at Ujazd prompted a re-examination of the previously interpreted palaeoecology of marginal-marine facies of the

Lower Devonian, and adds fish bottom feeding as an aspect of the benthic ecology in the environment. *O. tarnowskae* represents also evidence of sarcopterygian behaviour. Lastly, the trace fossil demonstrates the utility of ichnology in testing interpretations of sarcopterygian behaviour based on functional anatomy.

Demírcan, H. & Uchman, A. 2010. Kiss of death of a hunting fish: trace fossil *Osculichnus labialis* igen. et isp. nov. from late Eocene – early Oligocene prodelta sediments of the Mezardere Formation, Thrace Basin, NW Turkey. *Acta Geologica Polonica* – 60: 29–38.

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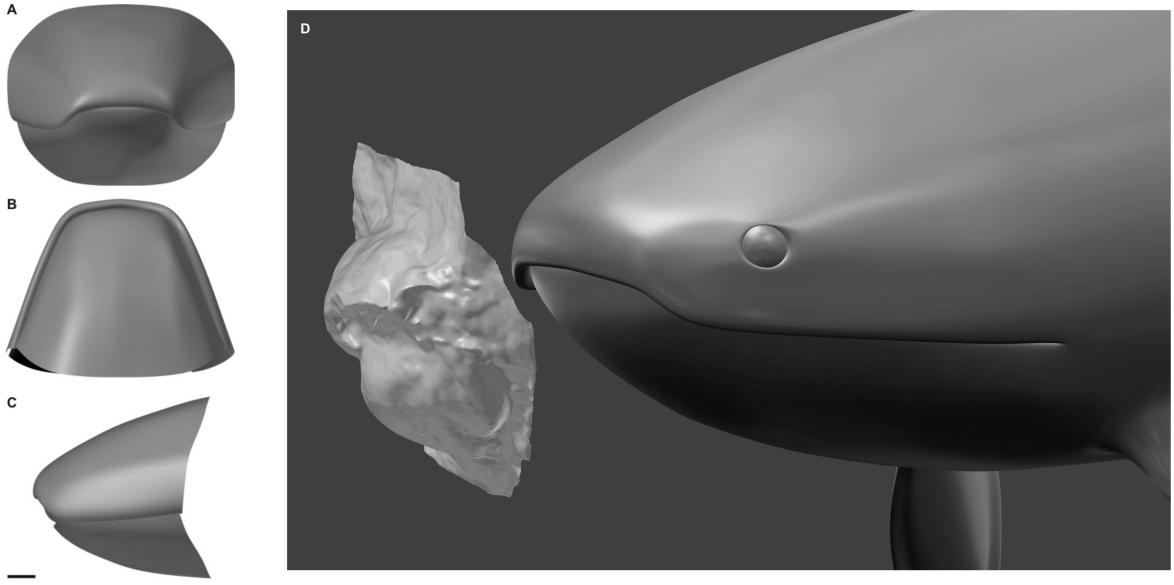
Figures

1. Three-dimensional reconstruction of the snout of the *Osculichnus tarnowskae* tracemaker. A. View *en face*. B. View from the bottom. C. Side view. D. Comparison of 3D reconstruction of the snout with trace fossil in lateral view. Scale bar = 1 cm (after Szrek et al. 2016).
2. Location and appearance of the investigated outcrop at Ujazd. A. Location map in the Holy Cross Mountains (HCM), Central Poland (modified from Kowalczewski, 1971). B. Studied section with trace fossil horizons. C. A photograph of the quarry with A and B trace-bearing horizons marked with arrows (after Szrek et al. 2016).



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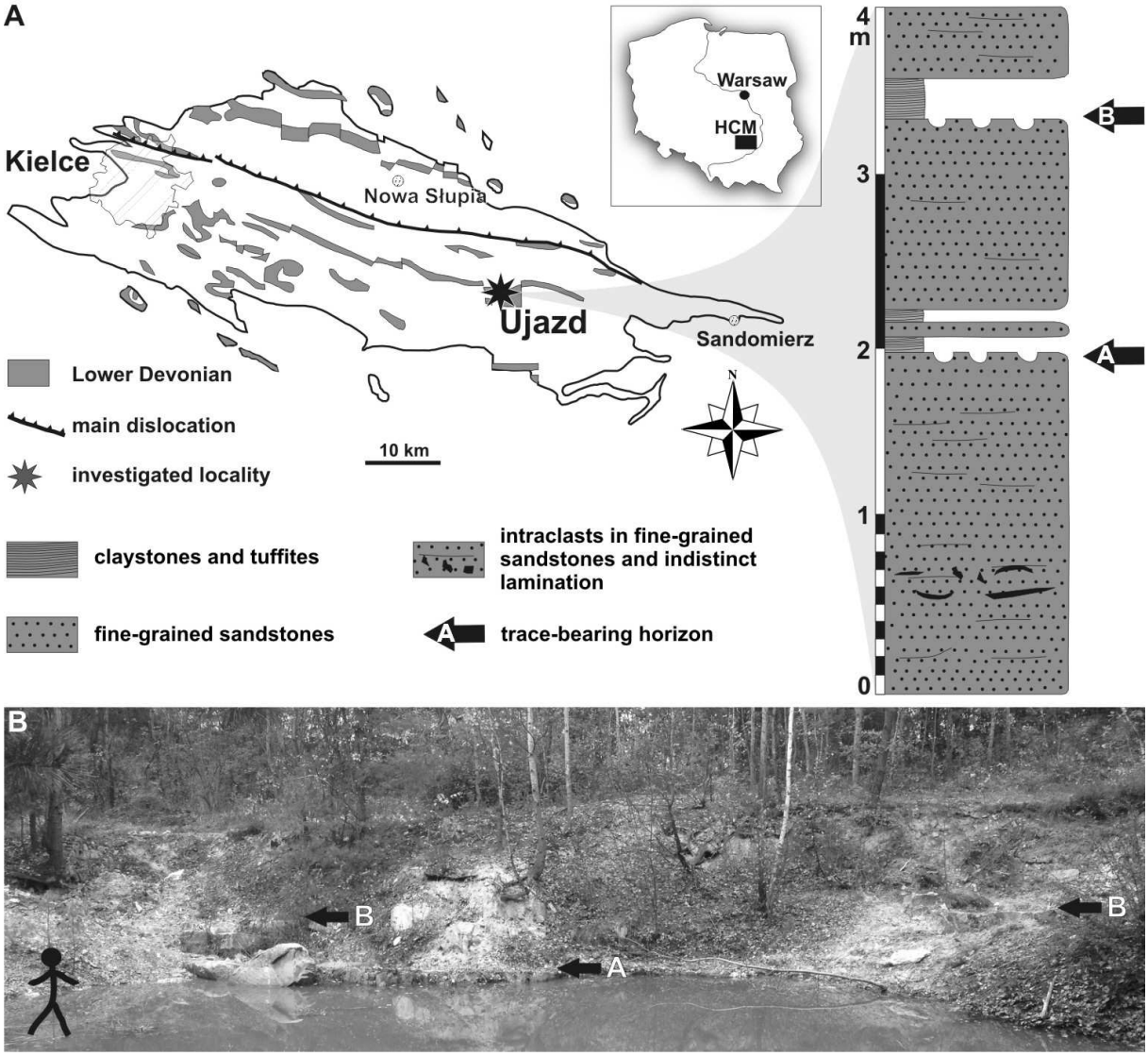
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Lower Devonian
main dislocation
investigated locality
claystones and tuffites
fine-grained sandstones
intraclasts in fine-grained sandstones and indistinct lamination
A
trace-bearing horizon
4 m
3
2
1
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B
A
B
B
A
B

2

Stop 5

Płucki. New insights in the old site.

Płucki is a village located near the NW outskirts of Łagów town in the central part of the Holy Cross Mountains, on the slope of Łagowica Valley, in the eastern fragment of the Kielce–Łagów Synclinorium.

The widely cited Płucki section is the only place in Central Europe where the Frasnian-Famennian boundary was regarded to occur within Kellwasser-like facies. Within the undisturbed sequence of the so-called Łagów Beds (Sobolew, 1912) there occur two horizons of black bituminous limestones, probably corresponding to the Lower and Upper Kellwasser-like Limestones (LKW and UKW, respectively) which are known from western Europe and Moroccan Meseta. The Frasnian-Famennian boundary is located in the middle of the upper horizon. Both Kellwasser horizons, occurring below a thin cover of soil. Numerous publications, starting from Makowski (1963), presented the geology and fauna of these horizons (see the references at the end).

The pit with the LKW is situated by the end of the village of Płucki (Fig. 1). The profile (about 1,5 m) consists of a set of marly limestones interbedding with marly shales. The LKW itself is a layer of black limestone, 5 cm thick, full of cephalopod shells (othocone nautiloids and goniatites) and occasional gastropods, bivalves, brachiopods, trilobites and placoderms. The characteristic feature is the concentration of fossils in the middle part of the layer. Here, the straight nautiloid shells display the unidirectional arrangement, suggesting the approximately E-W palaeotransport. Latest geochemical and palaeontological analyses (Rakociński et al. 2016) suggest that, during the Late Frasnian, deeper-water masses in the Łysogóry basin were mainly anoxic, but were interrupted by episodes of better oxygenated conditions. Episodic oxygenation of bottom waters promoted the rapid colonization of the seafloor by opportunistic shelly benthos, mostly buchiolid bivalves. These bivalves were affected by mass mortality upon the return to anoxic conditions.

The overlying part of the section is much less fossiliferous; in the overlying marls a few lenses with small brachiopods and bivalves were found. Both the sequence and the black limestone were known to Racki (1993), Racki *et al.* (2002) and Dzik (2002). The stratigraphic position of the LKW, Late *Palmatolepis rhenana* conodont Zone, was confirmed by Janiszewska *et al.* (2007) and Rakociński *et al.* (2016). Also the conodont biofacies and facies type correspond to the typical Lower Kellwasser Limestone of Germany (Ziegler & Sandberg, 1990).

The second outcrop (with the upper horizon, UKW) was made about 200 m SSE of the first one, near the edge of Łagowica valley. The outcrop is about 3 m deep and exposes limestones, marly limestones, marls, and shales. The sequence is strongly disturbed by the presence of a Devonian underwater landslide ascertained very recently (P. Szrek and S. Salwa, personal communication, 2014, in prep.). Allochthonous origin of all elements composing the horizon and mixed nature of the section forecloses to use the term “Upper Kellwasser Limestone” (*sensu* e.g. Klapper et al 1993) according to the discussed contemporary horizon in Płucki. The black Kellwasser-like limestone is about 0.5m thick and consists of several discontinuity events (Janiszewska et al., 2007; Szrek, 2007; Szrek and Ginter, 2007, 2008; Rakociński et al., 2016). The lower, entirely Frasnian part (up to 30 cm) is characterized by a marl at the bottom with gradual changes upwards into limestone. The middle part (up to 10 cm) is the most fossiliferous and is particularly rich in cephalopods and minute arthrodire placoderms. According to precise analysis of Janiszewska et al. (2007) the Frasnian–Famennian boundary is situated within this part of the horizon. The uppermost part entirely belongs to the Famennian and is characterized by numerous invertebrates and fishes.

Among the fossils from the upper Kellwasser of Płucki locality, where the biggest part of the described specimens come from, we ascertained following species: *Rhynchodus, Holonema, Oxyosteus, Leptosteus, Plourdosteus, Eastmanosteus, Brachyosteus, Selenosteus, Stenosteus, Pachyosteus, Rhinosteus, Microsteus* and *Aspidichthys*. There also occurs a new genus of Selenosteide and a new form of the big representatives of *Dunkleosteus* genus (Szrek & Wilk, in prep.). The analysis of the placoderm assemblage from Płucki also shown the similarity to its contemporary fauna assemblage from Bad Wildungen (Germany).

The observations (made according to the taphonomy) of the placoderms' plates led to the statement that the main impact on the processes of bone damaging was made by the mechanical factors (during slump event for instance), not the chemical influence of the sea water.

In several outcrops spanning the Frasnian-Famennian boundary beds in the Holy Cross Mountains, e.g., Wietrznia Quarry, an evident stratigraphic gap occurs on that boundary (Szulczewski, 1989). If such gap exists in the UKW at Płucki, it is negligible and probably impossible to be traced with the available biostratigraphic tools. Thus, the Płucki outcrop can be considered the best documenting site for the Frasnian-Famennian transition in Poland.

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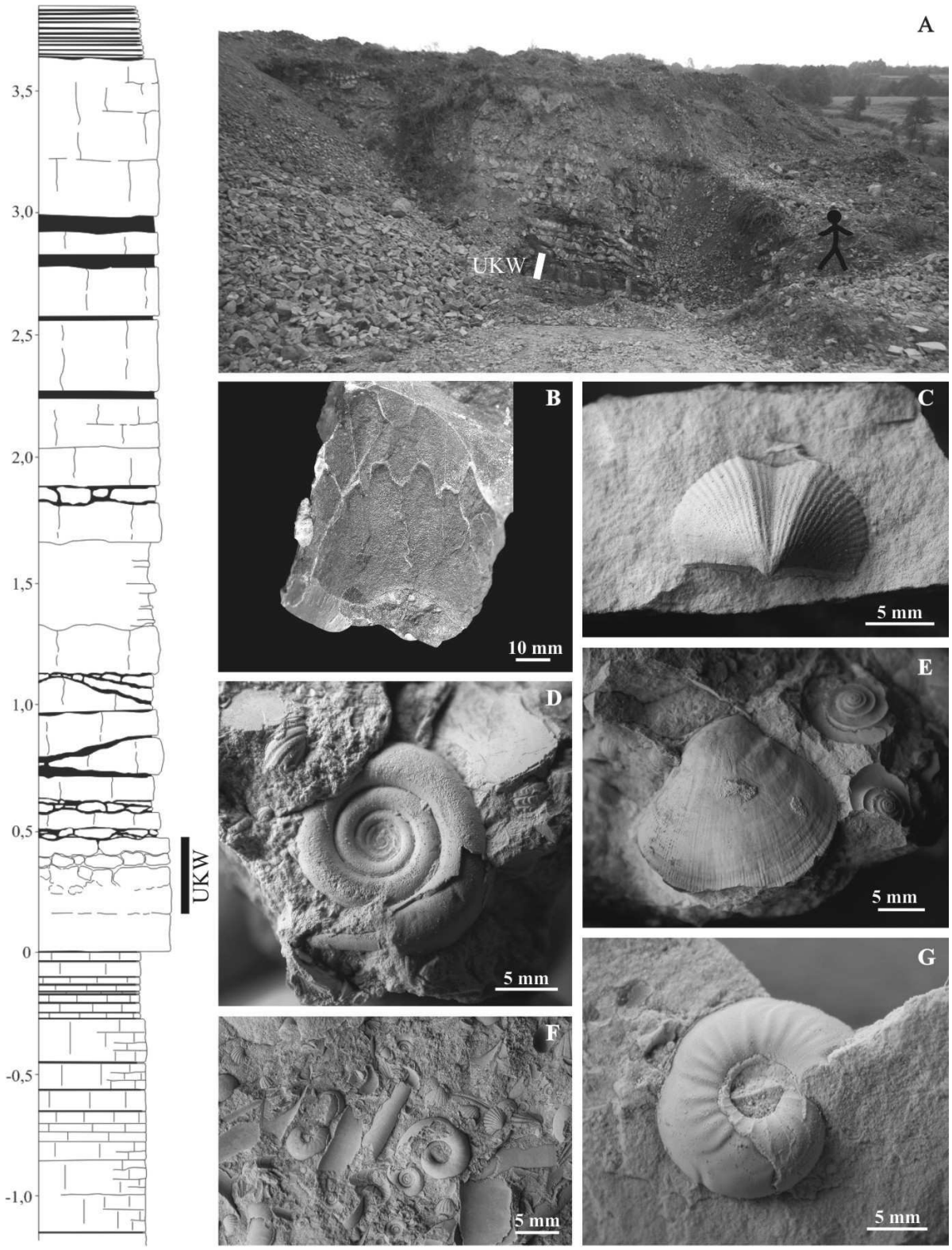
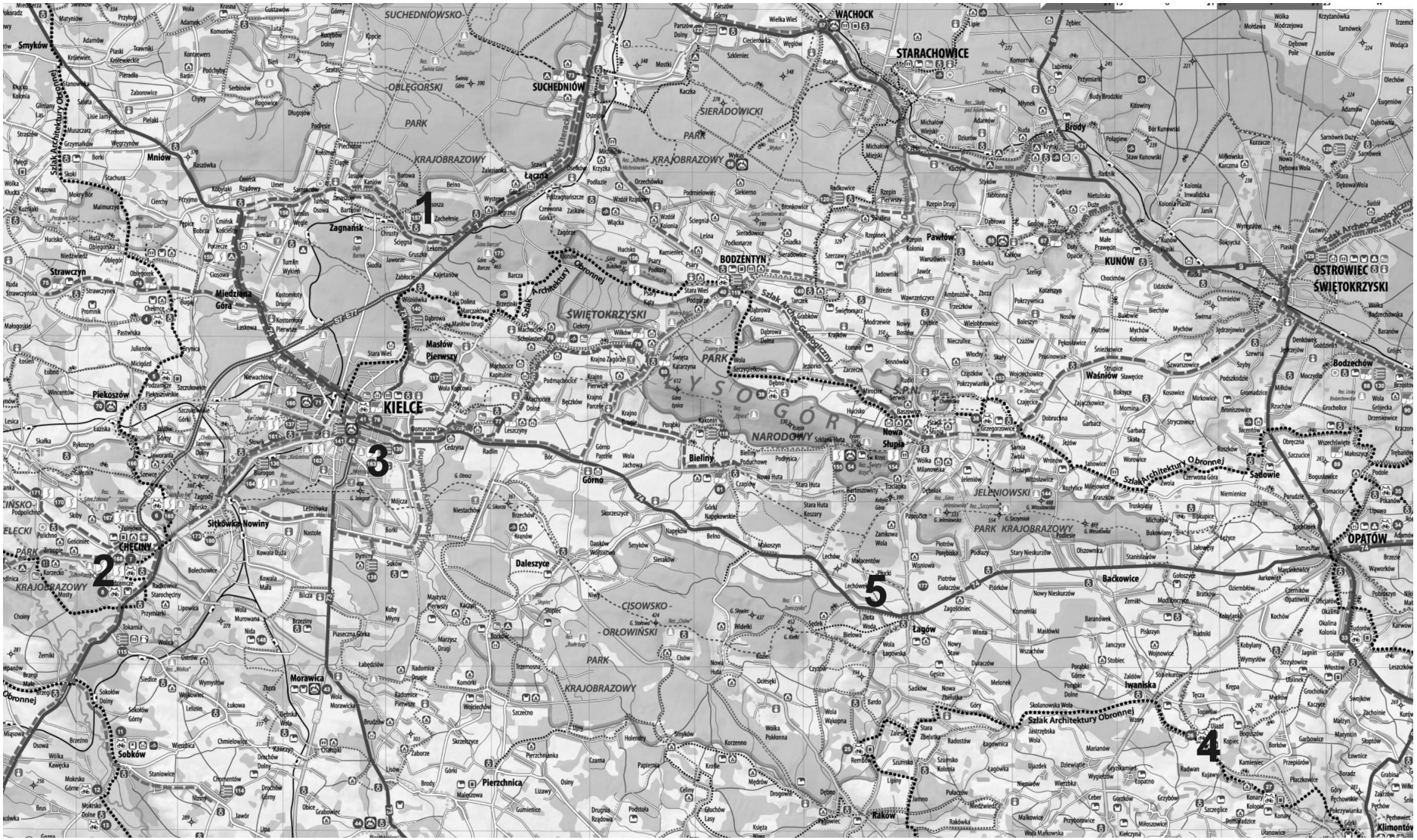


Geological profile of the outcrop with Upper Kellwasser-like horizon (UKW, drawn by K.Wójcik; for lower one see Szrek & Ginter, 2008). A. General view of the outcrop (Autumn 2016). B. Skull of a placoderm, *Pachyosteus* cf. *bulla*. C. Brachiopod, *Cyrtospirifer* sp. D. Goniatite, *Archoceras varicosum*. E. Bivalve, *Loxopteria* cf. *problematica*. F. Lower Kellwasser Limestone (LKW) with cephalopods. G. Goniatite, *Aulatornoceras* sp.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Raków
Pierzchnica
Morawica
Sobków
Sitkówka-Nowiny
Piekoszów
Miedziana Góra
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SUCHEDNIOWSKO-OBLĘGORSKI PARK KRAJOBRAZOWY
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ŚWIĘTOKRZYSKI PARK NARODOWY
JELENIOWSKI PARK KRAJOBRAZOWY
CISOWSKO-ORŁOWIŃSKI PARK KRAJOBRAZOWY
Szlak Architektury Obronnej
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Map of stops

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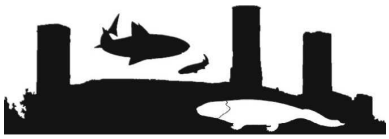
Appendix



Devonian dipnoans from Poland

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The material of dipnoans from the Devonian of Poland is sparse and it comes from few sites in Holy Cross Mountains (southeastern Poland).

First detailed study was done by Gorizdro-Kulczycka in 1950, who described four specimens from the Upper Devonian (Frasnian) localities – Kadzielnia, Wietrznia, Karczówka and Lipowa. The most interesting fossil is an almost complete lower jaw originally described as *Holodus santacrucensis*, assigned to *Holodipterus* by Moy-Thomas and Miles (1971). Along with flat tooth plates without radiating ridges some marginal tooth rows can be observed on the dentary of this specimen. This specimen is covered with cosmine on the lateral sides. The other material consists of three incomplete tooth plates.

Recent study of the Lower Devonian material has put a contribution to the knowledge on dipnoans also from the "Placoderm Sandstone". In the rich collection of the vertebrate remains there is a one fragment which has been attributed to dipnoan fish. It represents a posterior part of the lower jaw, probably right. Labial pit is well recognizable and the outer side is covered with cosmine. Taxonomic affinity of this specimen is difficult to resolve. Several dipnoan scales are also present in the "Placoderm Sandstone", some of them incorrectly attributed to *Porolepis* by Kulczycki (1960). Trace fossils (*Osculichnus tarnowskae*) are recently described from the contemporary beds of the same region and they were probably made by a lungfish broadly similar to *Dipnorhynchus* or *Chirodipterus australis* (Szrek *et al.*, 2016). It is probable that the jaw fragment belongs to the trace-maker.

Here we compare the Devonian dipnoans from Poland with other Devonian dipnoans and review their systematic affinity. We also present their paleogeographical distribution.

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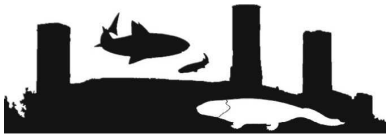

Acanthodian remains from the Permocarboniferous strata of Sudety Mountains, Poland

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Nearly 200 years ago first acanthodian remains were discovered in Wolbromów locality, Sudety Mountians. Since that time, new findings were subsequently reported from the proximate localities in Czech Republic (North-Sudetic Basin, Krkonose Piedmont Basin, Boskovice Basin) (Zajíc, 2005) and Germany (Saale Basin) (Heidtke, 2011). New species were recognized in those two regions, but the area of the type locality itself remained little known up till today.

Recent filed works in old Polish localities (Mastalerz, 1990, Raczyński and Mastalerz, 1996, Skrzycka et al. 2013) proofs that those sites have still potential to explore. One of the most interesting findings is a nearly complete acanthodian fish. It comes from Okrzeszyn, located nearby Wolbromów type locality but in Intra-Sudetic Basin. Among other recently found remains are patches of scales and disarticulated bones or isolated scales and bones.

The articulated specimen measures 7,5 cm, is missing the tail and has poorly preserved and incomplete head with mostly disarticulated bones. Specimen is laterally compressed and preserved in twisted, possibly in U-shaped position, with head pressed to the side of the trunk. In the view of new data with more species recognized over the years the new specimens need to be compared with both newly discovered and the holotype material.

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